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NOTE ON ARGENTINE CHARAS

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It may be conceded that the Charophyte-flora, even in those countries most thoroughly explored botanically, is none too well known. In countries such as Argentina, large in area and varied in climate, our knowledge is very much less, and is based almost entirely on incidental collections of the plants made by those who were primarily interested in gathering quite different material.

The scarcity of Charophyte-material is clearly indicated by the paucity of papers mentioning any such plants from Argentina. Alexander Braun (1882) mentioned *Chara foetida* A. Br. as occurring in that country, and referred to a form of *Chara Martiana* from there also. Spegazzini (1883) listed, as occurring there, ten species of these plants (6 *Nitella*, 1 *Lamprothamnus*, and 3 *Chara*, with several varieties and forms in addition), three being described as new species. It may be added that a few papers record the occurrence of additional species from the several countries bordering Argentina. All these suggest that despite the very small number of references to these plants they may be found to be of rather frequent occurrence there.

The present note results from the study of a small collection of five folders of the genus *Chara*, collected in October and November 1938, and January 1939, by W. J. Eyerdam, A. A. Beetle, and E. Grondona. As is not unusual with this group of plants, much of the material was received in a badly fragmented condition; however, species determination of all specimens was easily possible.

Three of the plants proved to be *Chara foetida* A. Br., noted above as occurring there. The condition of the specimens was such that determination of varieties or forms seemed inadvisable. Indeed the question might be raised as to whether the present state of knowledge of Charas is sufficiently ample to justify the establishment of too many varieties. Certainly casual examination of the three plants might lead to a conclusion that one had before him at least two species and perhaps a variety of one, making allowances for the immature condition of one of them. Yet in every particular — stem cortication, stipular crown, nature of branches, and fruit details — they closely resemble each other, varying only in the amount of incrustation, in the nature of the bracts, and more noticeably in the size of the specimens.

One of the two remaining folders was rather confusing on first examination, owing to the presence of two distinct species, *Chara Martiana* A. Br. and fragments of what seemed to be an atypical form of *Chara foetida* A. Br. The *Chara Martiana* was a male specimen.

The fifth folder contained a plant which proved to be a real puzzle. The plants were collected from "a still pond, in soft clay mud," and were noted to have "fruit very malodorous." The specimens (Fig. 1) were all small, the largest just over 10 cm. tall, of quite delicate appearance, and each of several slender spreading branches. The incrustation, present throughout the plant, was thin and inconspicuous, giving it a rather brownish-green color (dried specimens).

The stems are rather irregularly tripli-corticate (Fig. 3b), and 0.5–0.62 mm. in diameter, the primary cells usually slightly more prominent than the secondary. No spine cells occur, but only small internodal cells. The stipular crown (Fig. 3a) comprises a single row of rather irregularly arranged cells, twice the number of leaves at the node, each cell rounded or slightly elongate. Leaves 8–10 in a whorl, up to 1.3 cm. long, comprising 6–9 segments, the last of which is a very short, conical cell. Many leaves are completely ecorticate; in others, one, two, or the three lowest nodes may be corticated. The nature of the cortication (Fig. 2b) is in no way correlated with the node in which the leaf occurs, there occurring every conceivable variation from whorls of leaves all entirely ecorticate to those in which the lowest segments of every leaf are corticated. The bracteoles are likewise quite variable in number and in length, but occur only at the lower internodes, usually only on those bearing sporangia. Those subtending the sporangia are all cylindrical, with abruptly tapering ends, and may considerably exceed the sporangia in length. Those opposite the sporangia are much reduced, often to inconspicuous short conical cells. The antheridia, found only in the youngest leaves near the stem apex (Fig. 2c), are 280–320 μ in diameter; they are soon deciduous. The sporangia occur on the lower two to three internodes, and are 820–860(–900) μ long and 410–425 μ in diameter. The oöspores are dark brown, have 14–15 spiral ridges on the surface and are 600 μ long and 325 μ in diameter. The wall between the ridges is quite plane.

This plant has many points in common with *Chara Curtisii* T. F. Allen, *Ch. delicatula* Ag., *Ch. hydropitys* A. Br., and *Ch. leptopitys* A. Br. From all these it is set off by the absence of spine cells, by its poorly developed stipular crown of a single row of scarcely elongated cells, and by the nature of the cortication of the leaves. From other described Charas it is much more completely separate. It is therefore now described as a new species.

Chara leiopytis sp. nov.

Monoica, tenera et flexilis, leniter incrustata 10 cm. longa; caule 0.5–0.62 mm. in diam., triplo-corticatis, aculeis nullis sed cellulis verruciformibus; corona stipulari duplici foliorum numero, ex unica cellularum paullo elongatarum vel rotundatarum serie inaequaliter disposita; verticillis foliorum e foliis 8–10 compositis, 1.3 cm. longis, geniculis 6–9, articulis omnibus ecorticatis vel infimis 1–3 corticatis, corticatis ecortica-

tisque saepe in eodem verticillo; geniculis infimis bracteiferis, bracteis inaequalibus, longis cylindricis, apicibus conicis vel breviter conicis; antheridiis 280–320 μ in diam. mox caducis; sporangiis solitariis, oblongis, 820–860(–900) μ longis, 410–425 μ in diam.; oosporis 600 μ longis, 325 μ in diam., 14–15-gyratis, inter gyros planis.

Argentina: In stagnis ad argillam teneram, in Prov. Jujuy, Depto. San Pedro.

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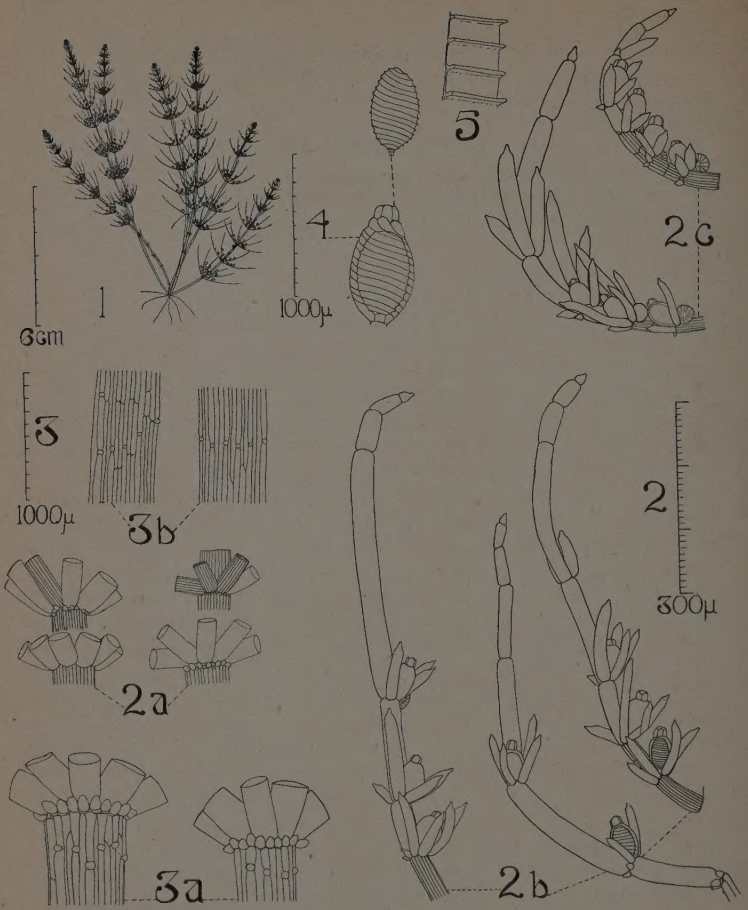
LITERATURE CITED

1882. **Braun, A.** Fragmente einer Monographie der Characeen. Edited by O. Nordstedt. Abhandl. K. Akad. Wiss. Berlin **1882.** 211 pp. 7 *pl.*

1883. **Spegazzini, C.** Characeae Platensis. Anal. Soc. Cient. Arg. **15:** 1–14.



Chara leiopytis Whelden n. sp.

Fig. 1. Habit of plant. **Fig. 2a.** Two illustrations of successive whorls, showing irregularities in branch cortications. **Fig. 2b.** Three branches showing irregularity of cortication, of node length, and of bracteoles. **Fig. 2c.** Two branches near apex of stem bearing antheridia. **Fig. 3a.** Two stem nodes showing stipular crown. **Fig. 3b.** Details of stem cortication. **Fig. 4.** Sporangium and oögonium. **Fig. 5.** Detail of wall of oögonium.

The magnification of each figure is given by an appropriately numbered scale.

NEW MOSSES FROM TIERRA DEL FUEGO

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About ten years ago I had the privilege of studying an extensive collection of mosses made by Dr. H. Roivainen in his capacity as botanist with the scientific expedition of the Finnish Geographical Society to Tierra del Fuego in 1928–29. All of the material was returned to Finland and subsequently I received a complete series of specimens including the types of many new species which resulted from the study, all of which are now in my herbarium.

In 1937 Dr. Roivainen published the results of his bryological investigations relating to Sphagnaceae, Andreaeaceae, Fissidentaceae, Ditrichaceae, Seligeriaceae and Dicranaceae.[1] This was to be followed by treatments of the succeeding groups but since then the unsettled conditions in Europe and especially in Finland have not only prevented further publications but have made it highly uncertain when, if ever, we may expect to have the remaining results of Dr. Roivainen's personal observations and studies. Meanwhile it seems advisable to record the descriptions of the new species, many of which are of the utmost interest.

DICRANACEAE

Chorisodontium sericeum Bartr. sp. nov.

Caespites densi, aureo-lutescentes, inferne fusci. Caulis ad 2 cm. altus, haud tomentosus, ramosus. Folia caulina circa 5 mm. longa, superne falcato-secunda, ovato-lanceolata, concava, sensim in acumen artistatum planum apice denticulatum attenuata; costa pallida, ad basin 50 μ lata, excurrente; cellulis alaribus distinctis, sequentibus linearibus, sinuosis, superioribus subquadratis vel oblongis. Folia perichaetialia e basi longe convoluta, subulata; seta 2.5 cm. longa, rubra, theca erecta, cylindrica; peristomium destructum. Caetera ignota.

Chile: Prov. de Magellanes, Isle Clarence, Puerto Beaubasin, ad saxa, No. 2297 **type.**

While similar to *C. lanigerum* (Besch.) Broth., this species seems to be constantly distinct in the flat, sharply toothed leaf tip, the narrower costa, and the stems almost devoid of either radicles or tomentum.

POTTIACEAE

Molendoa fuegiana Bartr. sp. nov.

Sat robusta, dense caespitosa, olivaceo-viridis, inferne fuscescens. Caulis circa 1.5 cm. altus, ramosus, inferne tomentosus, dense foliosus. Folia sicca contorta, madida arcuato-

[1] Roivainen, H. Bryological Investigations in Tierra del Fuego. Ann. Bot. Soc. Zool.-Bot. Fenn. Vanamo, 9(2):v–x; 1–58. 1937.

patula, flexuosa, comalia stellata, ad 2.5 mm. longa, lineari-lanceolata, canaliculata, acuminata; marginibus erectis, undulatis, papilloso-crenulatis; costa valida, fusca, ad basin 100 μ lata, excurrente, mucronata, apice papillosa; cellulis superioribus rotundato-quadratis vel transverse dilatatis, chlorophyllosis, obscuris, dense papillosis, marginalibus hic illic bistratosis, inferioribus linearibus, rectangularibus. Caetera ignota.

Fuegia media: Lago Blanco, Puesto de los Indios, ad rupes, Nos. 162*a*, 163 **type,** 173.

As compared with the description of *M. boliviana* Broth. and *M. Herzogii* Broth. the leaves of *M. fuegiana* are appreciably longer while in *M. andina* Mitt. the leaves are narrower below and the upper leaf cells smaller and not transversely elongate.

Didymodon ampliretis Bartr. sp. nov.

Caespites compacti, virides, inferne fuscescentes. Caulis 1–1.5 cm. altus, pluries divisus, gracilis. Folia sicca parce contorta, humida erecto-patentia, ovato-lanceolata, canaliculata, sensim angustata, apice subobtusa; marginibus minute papilloso-crenulatis, medium versus anguste reflexis; costa valida, infra summum apice evanida; cellulis superioribus rotundato-quadratis, dense chlorophyllosis, obscuris, papillosis, marginalibus bistratosis, inferioribus rectangulis, pellucidis. Caetera ignota.

Fuegia media: Lago Fagnano, punta Pizzaro, ad rupes, No. 1217 **type;** Fuegia bor.: Estancia Esperanza, No. 427.

By comparison with *D. diaphanobasis* Card. of Mexico, the upper leaf cells of *D. ampliretis* are much more chlorophyllose and obscure while the basal cells are shorter with more firm, pellucid lateral walls.

Tortula robusta Hook. & Grev. var. **laxa** Bartr. var. nov.

Cellulis laminalibus laxioribus, 15–20 μ latis, grosse papillosis.

Fuegia media: Lago Linch, in silva paludosa, No. 189; Lago Linch, Cerro Chico, in reg. alp., No. 1357; Estancia Cameron, Puesto Medio, in prato humido, No. 1895 **type;** Fuegia occidentalis: Fjordo de Agostini, Bahia Groth Hansen, No. 254; Fjordo Martinez, ad rupes sericiticas, No. 583.

The collections referred here differ from typical *T. robusta,* as I understand it, in the large, lax, thin-walled cells of the upper lamina which are coarsely papillose with C-shaped papillae. The costa is smooth to papillose on the back. The leaves are narrower than those of *T. rivularis* Dus. and not as strongly serrate, while the cells are appreciably larger than in *T. pseudorobusta* Dus.

GRIMMIACEAE

Grimmia scabripes Bartr. sp. nov.

Autoica, caespitosa, sat robusta, fusco-viridis. Caulis prostratus, 3–4 cm. longus, ramosus. Folia caulina conferta, sicca appressa, humida erecto-patentia, ovato-lanceolata, concava, sensim in pilum hyalinum spinulosum attenuata, 2–3 mm. longa, 1 mm. lata; costa valida, in pilum producta, dorso papillosa; marginibus integris, toto fere longitudine late recurvis; cellulis superioribus rotundatis, altissime papillosis, hic illic bistratosis, margines versus 3–4 stratosis, inferioribus rectangularis, parietibus maximus incrassatis sinuosisque. Folia perichaetialia erecta, majora, costa angustiore; capsula immersa, breviter pedicellata, oblonga; peristomium aurantiacum, dentibus lanceolatis, integris; sporae lutescentes, laeves, diam. 8–10 μ.

Chile: Prov. de Nuble, Recinto, Las Trancas, ad truncos Nothofagi antarcticae, alt. 1150 m., No. 1003 **type.**

Readily distinguished from any of the forms of *G. apocarpa* and, in fact, from any of the species of the section *Schistidium* by the coarsely papillose leaf cells. A cross section of the leaf shows the papillae to the best advantage but they may be clearly seen in profile on the roll of the leaf without sectioning.

Rhacomitrium limbatum Bartr. sp. nov.

Robustum, dense caespitosum, nigrescens. Caulis erectus, ad 4 cm. altus, irregulariter divisus. Folia conferta, sicca erecta, parce flexuosa, humida patentia, 3.5–4 mm. longa, ovato-lanceolata, sensim acuminata, superne carinata, toto ambitu limbo lato incrassato circumducta; marginibus integris, inferne reflexis, superne planis; costa valida, excurrente; cellulis inferioribus linearibus, parietibus incrassatis, valde sinuosis, superioribus brevioribus, oblongis, costa versus bistratosis, margines versus 6–9 seriatis 3–4 stratosis. Seta 5–6 mm. longa; peristomii dentes rufescentes, ad basin divisi, papillosi; sporae papillosae, diam. 15–22 μ.

Fuegia occid.: Fjordo Finlandia, Brazo Aina, ad saxa, No. 502; Fjordo Martinez, ad rupes uliginosas, No. 594; Fjordo de Agostini, Bahia Groth Hansen, No. 2268; Chile: Prov. de Magellanes, Fuegia occid., Monte Buckland, alt. 500 m., Nos. 2084a, 2644; Isla Clarence, Puerto Beaubasin, ad saxa, Nos. 2313, 2316 **type.**

This exceedingly fine and interesting species is immediately distinguished from any of the forms of *R. crispulum*, and also from any member of the genus with which I am familiar, by the broad, fleshy leaf border extending from the apex almost to the insertion.

Rhacomitrium scabrifolium Bartr. sp. nov.

Robustum, aureo-lutescens. Caulis ad 8 cm. longus, irregulariter divisus, ramis breviter ramulosis. Folia 3.5 mm. longa, sicca erecta, humida erecto-patentia, ovato-lanceolata, plicata, superne canaliculata, sensim in pilum hyalinum denticulatum producta; marginibus papilloso-crenulatis, reflexis; costa depressa, angusta, ad medium folii evanida; cellulis omnibus elongatis, linearibus, papillosis, parietibus incrassatis, lutescentibus, valde sinuosis. Caetera ignota.

Chile: Prov. de Magellanes, Fuegia occid., Monte Buckland, alt. 500–700 m., No. 241; Puerto Yarton, Pico Nariz, reg. alp. No. 820; Fjordo Finlandia, Brazo Aino, No. 1970; Fjordo de Agostini, No. 2068 **type;** Bahia Sarmento, No. 2465.

The combination of plicate leaves and papillose leaf cells will separate this species from any of its Fuegian associates. In *R. ptychophyllum* Mitt. of New Zealand, the leaves are plicate but the short lateral branchlets are lacking and the leaf cells are smooth.

FUNARIACEAE

Funaria (Entosthodon) **pungens** Bartr. sp. nov.

Autoica, pusilla, gregaria, lutescente-viridis. Caulis 3–5 mm. altus, inferne radiculosus. Folia ovato-oblonga, acuminata, concava, comalia 2.5–3 mm. longa; marginibus integris, erectis, saepe ad basin uno latere inflexis; costa tenui, longe ab apice folii evanida;

cellulis superioribus oblongo-hexagonis, ad 50 μ latis, inferioribus rectangularibus. Seta erecta, rubella, ad 18 mm. longa; theca erecta, pyriformis; peristomium simplex, dentes rufi, papillosi; sporae fuscescentes, diam. 25–28 μ.

Fuegia occidentalis: Fiordo Martinez, Bahia Sarmento, No. 2358 **type.**

This species will be distinguished from *F. chiloensis* Mitt. by the sharply acuminate leaves and the broader and laxer areolation of the upper part of the leaf.

SPLACHNACEAE

Tayloria magellanica (Brid.) Mitt. var. **gigantea** Bartr. var. nov.

Caules 18–20 cm. alti, dense compacti.

This seems to be only an extremely robust form with densely tufted parallel stems, up to 2 dm. high, showing very clearly the zones of growth. The development is unusual and in this condition the plant is an exceptionally fine one.

Fuegia occidentalis: Fjordo Finlandia, prope Montem Nylandiam, No. 1745 **type.**

BRYACEAE

Mielichhoferia multiflora Bartr. sp. nov.

Synoica; flores plures stipitati. Caespites compacti, superne lutescente-virides, nitidi, inferne dense fusco-radiculosi. Caulis erectus, ad 2.5 cm. altus, dense julaceo-foliosus. Folia erecta, imbricata, ovato-lanceolata, acuminata, carinato-concava; marginibus erectis, superne denticulatis; costa valida, infra apicem folii evanida; cellulis anguste rhomboideis, basilaribus rectangularibus. Seta 8–10 mm. longa, lutescente-rubra; theca inclinata, asymmetrica; annulus latus; endostomium pallidum, corona basilaris humilis, processus angusti, linea divisurali distincti; operculum depresse conicum, apiculatum; sporae lutescentes, diam. ad 20 μ.

Chile: Prov. de Nuble, Cordillera de Chillan, alt. 2200 m., No. 1699 **type.**

In some respects the details of this species closely approximate the description of *M. leptoclada* C. M., but in *M. multiflora* the leaves are erect and closely imbricated and the segments of the endostome show a median line.

The numerous stalked flower buds are conspicuous and may be a good diagnostic character. While the fertile flowers are synoicous, the remaining undeveloped buds are often composed entirely of antheridia. Either the archegonia in these buds are abortive or the inflorescence is heteroicous.

Bryum (Cernuiformia) **Roivaineni** Bartr. sp. nov.

Synoicum; caespitosum, caespitibus densiusculis, sordide viridibus. Caulis ad 5 mm. altus, basi fusco-tomentosus, innovando-ramosus. Folia ad 3 mm. longa, ovata, acuta, haud decurrentia, concava; marginibus anguste recurvis, integris; costa crassa, fusca, infra apicem folii evanida vel percurrente; cellulis oblongo-hexagonis, firmis, basilaribus rectangularibus, concoloribus, marginibus elongatis, limbum biseriatum, fuscescentem efformantibus. Seta circa 2 cm. longa, rubra; theca nutans, oblongo-piriformis, sicca deoperculata, haud constricta; exostomii dentes fusco-lutei, endostomum sordide luteum, papillosum, processus angusti, exostomio adhaerens; sporae 18–22 μ in diam.

Chile: Prov. de Magellanes, Fuegia occid., Fjordo Finlandia, Brazo Aino, No. 2110 **type.**

This species seems to be distinct from both *B. austro-chilense* and *B. dicarpum* in the broader, less sharply pointed leaves and the thick, strong costa.

Bryum (Inclinatiformia) **fuegianum** Bartr. sp. nov.

Synoicum; gracile, caespitosum, caespitibus mollibus, pallide viridibus, inferne fuscescentibus. Caulis erectus, 2 cm. altus, gracilis, innovando-ramosus, innovationibus erectis, circa 2 cm. longis, base radiculosis. Folia sicca erecta, contorta, humida erecto-patentia, spathulata vel obovata, breviter acuminata, usque ad 3 mm. longa, 1.5 mm. lata; marginibus inferne reflexis, integris; costa infra apicem folii evanida vel percurrente; cellulis laxis, teneris, oblongo-hexagonis, basilaribus rectangularibus, rubris, marginalibus elongatis, limbum 3–4 seriatum efformantibus. Seta tenuissima, rubra, 5–6 cm. longa; theca nutans; exostomii dentes fusco-lutei; endostomium hyalinum, papillosum, processus angusti, superne dentibus adhaerens, cilia 0, sporae 25 μ in diam.

Fuegia media: Puesto Medio de la Estancia Cameron, in palude, No. 8 **type.**

Bryum (Cernuiformia) **austro-chilense** Bartr. sp. nov.

Synoicum; caespitosum, viridibus, inferne fuscescentibus. Caulis ad 1 cm. altus, basi fusco-tomentosus, innovando-ramosus. Folia sicca erecta, contorta, late ovata, breviter acuminata, carinato-concava, circa 1.5 mm. longa; marginibus anguste reflexis; costa fusca, percurrente; cellulis laxis, oblongo-hexagonis, basilaribus rectangularibus, concoloribus, marginalibus elongatus, limbum biseriatum efformantibus. Seta ad 2 cm. alta, rubra; theca nutans, pyriformis, 3 mm. longa; exostomii dentes fusco-lutei, apice hyalini, endostomium pallide luteum, processus angusti, superne dentibus adhaerens, cilia 0; sporae papillosae, 25 μ in diam.

Chile: Prov. de Nuble, Cordillera de Chillan, alt. 2000–2200 m., Nos. 1042, 1043, 1693 **type.**

Perhaps near *B. obscurum* Card. & Broth. but in comparison with the description of this species, the leaves of *B. austro-chilense* are smaller, the costa percurrent and the leaves of the innovations not comose at the tips.

Bryum (Cernuiformia) **dicarpum** Bartr. sp. nov.

Species precedenti forsan affinis sed costa infra apicem folii evanida, sporis majoribus et theca pendula, microstoma.

Synoicous; similar in habit and vegetative characters to *B. austro-chilense* but the leaves slightly larger, up to 2.5 mm. long with the costa ending just below the apex; setae constantly two from the same perichaetium; capsules pendulous, small-mouthed; spores 32–35 μ in diam.

Fuegia bor.: Hotel Bouqueron, in loco paludoso, No. 317 **type.**

Bryum (Inclinatiformia) **macrosporum** Bartr. sp. nov.

Dioicum; caespitosum, caespitibus densis, viridibus. Caulis erectus, 3–5 mm. altus, superne comoso-foliosus, inferne fusco-tomentosus. Folia comalia late oblongo-ovata, acuminata, carinato-concava, sicca erecta; marginibus integris, anguste reflexis; costa rubra, in aristam usque 300 μ longam, levem excedente; cellulis rhomboideis, basilaribus rectangularibus, rubris. Seta circa 2 cm. alta, rubra; theca pendula, 1 mm. longa, oblonga; exostomii dentes lutei, apice hyalini, endostomium hyalinum, processus

angusti, fenestrati, ciliis interpositis 3, parum brevioribus, haud appendiculatis; sporae lutescentes, papillosae, 30 μ in diam.

Chile: Prov. de Magellanes, Fuegia media, Lago Fagnano, Punta Pizzaro, No. 1211 **type.**

By the dioicous inflorescence this species is allied to *B. vernicosum* Dus. and *B. Hatcheri* Dus. but is distinct from both in the well-developed cilia of the inner peristome and the larger spores.

Bryum (Pseudotriquetra) **brachycarpum** Bartr. sp. nov.

Dioicum; caespitibus densis, pallide viridibus, intus fuscescentibus. Caulis erectus, innovando-ramosus. Folia ovata, breviter acuminata, limbata, ad 2.5 mm. longa; marginibus inferne anguste revolutis, summo apice minute denticulatis; costa inferne rubra, percurrente vel breviter excedente; cellulis rhomboideis, basilaribus oblongis, rubris, marginalibus elongatis, limbum 3–4-seriatum efformantibus. Seta 5–6 cm. longa, tenuis, rubra; theca pendula, 2.5 mm. longa, piriformis; cilia appendiculata; operculum convexum, apiculatum; sporae lutescentes, diam. 18–20 μ.

Fuegia media, Estancia la Marina, in palude, No. 677 **type.**

This species is apparently near *B. zeballosicum* Card. & Broth. but is clearly distinguished from this and any of the allied group by the much longer setae and the short, pyriform capsules with the neck only about half as long as the sporangium.

Bryum (Caespitibryum) **pauperculum** Bartr. sp. nov.

Dioicum; caespitosum, caespitibus densis, superne lutescenti-viridibus, intus fuscescentibus. Caulis vix 1 cm. longus, inferne fusco-radiculosus. Folia sicca appressa, humida erecto-patentia, triangulari-lanceolata, ad 2.5 mm. longa, sensim acuminata; marginibus fere ad apicem revolutis, integris; costa valida, in aristam laevem excedente; cellulis oblongo-hexagonis, basilaribus rectangularibus, rubris, alarabis laxis, marginalibus elongatis, limbum indistinctum efformantibus. Seta circa 2 cm. longa; exostomii dentes pallide lutescentes, endostomium hyalinum, papillosum, cilia appendiculata; sporae minutissime papillosae, fuscae, diam. circa 30 μ.

Chile: Prov. de Magellanes, Fuegia occid., Cabo San Pablo, Nos. 658 **type,** 670.

This species evidently stands in close proximity to *B. caespiticum* but the leaf outline is different, the margins and the arista are entire and the spores twice as large.

Bryum (Rosulata) **pseudothyridium** Bartr. sp. nov.

Dioicum; robustum, caespitosum, caespites densi, pallide lutescente-virides, nitidiusculi. Caulis erectus, dichotome innovans, dense rufo-tomentosus, ad 4 cm. altus. Folia ad apicem innovationem congesta, sicca erecta, flexuosa, spiraliter contorta, humida erecto-patentia, oblongo-obovata, apiculata, late limbata, ad 5 mm. longa; marginibus fere ad apicem revolutis, apicem versus remote denticulatis; costa crassa, basi rubella, in apiculum laevem excedente; cellulis ovato-hexagonis, basilaribus rectangularibus, infimis rubris, marginalibus linearibus, multiseriatis, limbum latum distinctum efformantibus. Seta ad 2.5 cm. longa, rubella, flexuosa; theca nutans vel pendula, oblongo-cylindrica, brevicollis, circa 3 mm. longa; operculum conicum, apiculatum; exostomii dentes fusco-lutei, apice hyalini, 0.6 mm. alti, endostomium pallide luteum, papillosum, corona basilaris alta, processus angusti, rimosi, cilia 3, valde appendiculata; sporae minute papillosae, diam. 12 μ.

Chile: Prov. de Magellanes, Fuegia occid., Puesto Yarton, loco uliginoso, No. 893 **type;** Fuegia media, Rio Bueno, Nos. 386, 1089.

An unusually handsome moss which is distinct from *B. Lechleri* C. M. and *B. andicola* Hook. in the more elongate and robust stems and the broad leaf border, up to 150 μ wide in the upper half of the leaf and composed of 8–15 rows of narrow linear cells.

BARTRAMIACEAE

Philonotis luteola Bartr. sp. nov.

Caespites compacti, pallide lutescente-virides. Caulis 5–6 cm. altus, inferne parce radiculosus, ramosus, ramis gracilis, laxifolius. Folia erecta, oblongo-ovata, breviter acuminata, haud plicata 2–2.5 mm. longa; marginibus planis, superne serrulatis; costa lata, male limitata, infra apicem dissoluta, dorso superne papillata; cellulis omnibus laevibus, laxiusculis, superioribus rhomboidalibus, inferioribus longioribus, marginalibus haud distinctis. Caetera ignota.

Fuegia media: Estancia Vicuna, Puesto 20, Cerro Fuentes, reg. alp., No. 734 **type.**

The unbordered leaves, broader costa and absence of any differentiated marginal cells at the basal angles will at once separate this species from any of the forms of *P. vagans*. It is distinguished from *P. acicularis* (C. M.) by the plane margined leaves and from both *P. varians* Card. and *P. parallela* Dus. by the costa ending below the apex.

Breutelia angustiretis Bartr. sp. nov.

Caespites densi, nitidi, superne lutescente-virides, inferne fusci, dense rufo-tomentosi. Caulis 4–5 cm. altus, irregulariter ramosus. Folia erecto-patentia, subflexuosa, e basi ovata, plicatula sensim longissime cuspidata, ad 4.5 mm. longa; marginibus integris, e basi anguste recurvis, superne planis; costa angusta, percurrente vel excurrente; cellulis omnibus anguste linearibus, laevibus, parietibus incrassatis, lutescentibus, infimis brevioribus, rubellis, parietibus sinuosis. Fructus ignotus.

Fuegia occidentalis: Fjordo Martinez, Bahia Pluschow, Nos. 592 **type,** 1136; Chile: Prov. de Magellanes, Isla Dawson, Puerto Valdez, in silva humida, Nos. 1326, 2563.

This species and *B. chrysura* (C. M.) Broth. are closely allied to *B. integrifolia* (Tayl.) Jaeg. A critical study of this group may show that the specific characters are too unstable to afford any practical basis for classification.

ORTHOTRICHACEAE

Macromitrium (Teichodontium) **coriaceum** Bartr. sp. nov.

Laxe caespitosum, lutescente-viride, intus fuscescens. Caulis repens, dense ramosus, ramis suberectis, usque ad 1 cm. longis, ramulosis. Folia sat densa, sicca erecta, contorta, humida erecto-patentia, lanceolata, plicata, breviter acuminata, superne carinata, 1.5–2 mm. longa; marginibus superne denticulatis; costa sub apice evanida; cellulis superioribus ovalis, incrassatis, laevibus, basilaribus anguste rectangularibus, valde incrassatis. Seta erecta, laevissima, 7–8 mm. longa; theca laevissima, oblongo-cylindrica, exothecio coriaceo; exostomium circa 30 μ altum, dentibus inter se concretis, papillosis, endostomium exostomio majus, processus 32, lati, obtusi, dense papillosi; calyptra nuda, laciniata; sporae papillosae, diam. 50–60 μ.

Chile: Prov. de Chiloe, Puerto Barroso de la Penins, Tres Montes, Nos. 1563, 1570 **type,** 1588, 1628.

Clearly distinguished from *M. Rushyanum* E. G. Britt. and *M. macrosporum* Herz. by the longer segments of the inner peristome and the naked calyptrae.

LEMBOPHYLLACEAE

Camptochaete arbusculans Broth. *ex* Bartr.

Dioica; caespitosa, lutescente-viridis. Caulis sublignosus, bipinnate ramosus, ramis teretibus, saepe flagelliformiter attenuatis. Folia conferta, concava, imbricata, latissime ovata vel obovata, minute apiculata, 1.5 mm. longa, 1 mm. lata; marginibus erectis, superne denticulatis; costa variabilis, nunc simplex et fere ad medium folii producta, nunc brevis et binis vel nulla; cellulae anguste rhomboideae, laevissimae, apicales breviores, alares sat numerosae.

Chile: Prov. de Nuble, Recinto, Las Trancas, alt. 1200 m., No. 1600; Chile australis in montibus Cordillera de la Costa supra Angol oppidam in truncis arborum, Dusen No. 338, Nov. 11, 1896, **type.**

Roivainen's No. 1600 is exactly similar to Dusen's No. 338, issued as *Camptochaete arbusculans* Broth. which has been made available for comparison through the kindness of M. Theriot. The species is included by Brotherus in Ed. 2 of the Pflanzenfamilien but as the description seems never to have been published it may be validated by the above brief diagnosis.

The stem and branch leaves are not clearly differentiated. The leaves are very broadly ovate or obovate, minutely apiculate, alar cells rather numerous, upper cells small, parenchymatous, rhomboidal, median and lower cells narrower; margins erect, denticulate above; costa variable, short and double or even lacking, often single and extending nearly to mid-leaf. The variable costa is an anomalous character in *Camptochaete* but the plants are otherwise characteristic so I believe they may be included here under **Rigodiella** sect. nov. characterized as follows:

Folia caulina et ramea vix diversa; costa maxime variabilis, nunc simplex et bene evoluta, nunc binis et brevis vel nulla.

HOOKERIACEAE

Sauloma tenella (H. f. & W.) Mitt.

Fuegia media: Rio Bueno, in silva Nothofagi, No. 2008.

New to South America. The broad distribution of so many austral types which are common to New Zealand and the tip of the South American continent is again emphasized by the occurrence of this species in Fuegia.

AMBLYSTEGIACEAE

Hygroamblystegium: I think Reimers (Hedwigia **66**:71. 1926) is entirely justified in transferring the following species to *Hygroamblystegium*. They are certainly better placed here than in *Pseudoleskea*.

The group is a very intricate one and the distinctions so slight and inconstant that I doubt if they can be resolved into definite specific identities. The large series collected by Dr. Roivainen seems to be separable into two fairly distinct types as outlined in the tentative key presented below.

Leaves closely appressed
  Loosely tufted plants ..... **H. filum**
  Densely tufted plants, stems parallel ..... **H. filum** var. **compactum**
Leaves spreading or secund
  Habit rigid, leaves strongly secund, uncinate at tips **H. fuegianum** var. **secundum**
  Habit lax
    Costa short excurrent
      Very slender plants ..... **H. fuegianum** var. **gracilis**
      More robust plants
        Leaves erect-spreading or secund ..... **H. fuegianum**
        Leaves widely spreading ..... **H. fuegianum** var. **Skottsbergii**
    Costa long excurrent ..... **H. fuegianum** var. **excurrens**

Hygroamblystegium filum (C. M.) Reim.

Hygroamblystegium filum var. **compactum** Bartr. var. nov.

Caules elongati, ad 10 cm. longi, dense compacti, cellulae superiores breviter hexagonae.

Chile: Prov. de Magellanes, Fuegia media, Lago Linch, Cerro Chico, reg. alp., No. 1380 **type.**

An unusual form with long, parallel, densely tufted stems and short upper leaf cells.

Hygroamblystegium fuegianum (Besch.) Reim.

The following sporophyte characters are taken from No. 1016 which is in good fruit.

Seta slender, reddish, smooth, about 2 cm. long, twisted to the right when dry. Capsule cylindric, curved, constricted below the mouth when dry, urn 2 mm. long; peristome large, pale yellow; lid not seen; calyptra pale, early deciduous; spores smooth, 10–12 μ in diam.

Hygroamblystegium fuegianum var. **Skottsbergii** (Card.) Bartr. comb. nov.
Pseudoleskea fuegiana (Besch.) Card. var. *Skottsbergii* Card.

Hygroamblystegium fuegianum var. **excurrens** (Card. & Broth.) Bartr. comb. nov.
Amblystegium excurrens Card. & Broth.

Hygroamblystegium fuegianum var. **gracilis** (Card. & Broth.) Bartr. comb. nov.
Pseudoleskea fuegiana (Besch.) Card. var. *gracilis* Card. & Broth.

Hygroamblystegium fuegianum var. **secundum** Bartr. var. nov.

Caules rigidi. Folia saepe fortiter falcato-secunda.

Chile: Prov. de Magellanes, Fuegia media, Lago Fagnano, Punta Pizzaro, No. 1213 **type.**

Very different from any of the allied forms in the rigid, rather robust stems, uncinate at the tips and with the leaves clearly falcate-secund.

Calliergidium austro-stramineum (C. M.) Bartr. comb. nov.
Hypnum austro-stramineum C. M.

Dr. Grout (Moss Fl. N. Amer. **3**(2): 100. 1931) has advanced what seem to be adequate reasons for separating this group from *Drepanocladus*.

Calliergon sarmentosum (Wahlenb.) Kindb.

Very similar to the plants of the northern hemisphere in every way except that the apical leaves of the young branches and stems are more closely imbricated to form a terete tip ending in a cuspidate point.

BRACHYTHECIACEAE

Brachythecium longidecurrens Bartr. sp. nov.

Autoicum; lutescente-viride, nitidulum. Caulis irregulariter ramosus, ramis arcuatis. Folia dense conferta, scariosa, sicca imbricata, humida erecto-patentia, caulina e basi longe decurrente latissime cordato-ovata, in acumen breviusculum constricta, 1.5–1.7 mm. longa; marginibus inferne reflexis, superne planis, fere e base minute denticulatis; costa valida, ad 4/5 folii evanida; cellulis linearibus, inferioribus brevioribus et latioribus, alaribus rectangularibus, pellucidis. Folia ramea angustiora, sensim acuminata. Folia perichaetialia ecostata, in acumen patulum subito constricta; seta rubella, 2 cm. longa, superne scaberula; theca horizontalis, sicca arcuata, 1.5 mm. longa, fusca.

Chile: Prov. de Magellanes, Fuegia media, Rio Bueno, in silva, Nos. 2018 **type,** 2025, 2063.

These plants have something of the habit of *B. rivulare* Bry. Eur. but are immediately distinguished by the acuminate leaves, the longer costa, and the setae which are smooth below.

Brachythecium (Julacea) **micro-collinum** Bartr. sp. nov.

Autoicum; tenellum, pallide viride. Caules intertexti, depressi, irregulariter pinnati, ramis curvato-patulis. Folia minuta, sicca imbricata, humida erecto-patentia, concava, ovato-lanceolata, acuminata, haud decurrentia, circa 0.5 mm. longa; marginibus toto ambitu denticulatis; costa valida, ad 4/5 folii evanida, extremitate dentiformi; cellulis linearibus vel lineari-rhomboideis, basilaribus laxioribus, rectangulis, infimis ovalibus vel breviter rectangulis. Folia perichaetialia enervia, e base subvaginante in acumen abrupte constricta, marginibus ad basin integris, superne argute denticulatis; seta rubella, 6–7 mm. longa, laevissima; theca horizontalis, 1 mm. longa.

Chile: Prov. de Nuble, Recinto, in silva umbrosa, alt. 750 m., Nos. 954, 955 **type.**

Near *B. collinum* (Schleich.) but much smaller in every way and with a stouter, longer costa ending in a spine on the back. *B. arenarium* Card. & Broth. is described as having the stem leaves ending in a long, subulate acumen. This character, if constant, should preclude any confusion with *B. micro-collinum*.

PLAGIOTHECIACEAE

Plagiothecium nitidum (Hook. f. & Wils.) Bartr. comb. nov.

Leskea nitida Hook. f. & Wils.

I have outlined elsewhere (Manual of Hawaiian Mosses, p. 224. 1933) my reasons for thinking that *Catagonium* is a poorly defined genus. The above species does not appear to be generically distinct from *Plagiothecium*.

Calliergonella complanata Card. & Broth.

To judge from a fragmentary specimen of the type collection consisting of two stems and a few detached leaves which I have seen through the kindness of Dr. Linkola, is apparently one of the forms of *Eucatagonium politum* (Hook. f. & Wils.) with the leaves not clearly distichous.

SEMATOPHYLLACEAE

Sematophyllum aureo-nitidum Bartr. sp. nov.

Dioicum? Caespites depressi, sat densi, lutescente-virides, nitidi. Caulis ad 3 cm. longus, irregulariter ramosus. Folia conferta, falcata, e basi ovato-oblonga abrupte longe acuminata, ecostata, circa 2 mm. longa; marginibus planis, inferne integris, superne denticulatis; cellulis anguste linearibus, incrassatis, infimis lutescentibus, admodum porosis, alaribus 3–4, oblongis, vesiculosis, hyalinis vel lutescentibus. Folia perichaetialia ovato-oblonga, breviter acuminata; marginibus superne irregulariter denticulatis; seta rubella, laevissima, circa 12 mm. longa. Caetera ignota.

Chile: Prov. de Magellanes, Fuegia occid., Fjordo Martinez, ad rupes, No. 579; Fjordo Martinez, Bahia Sarmiento, No. 2351 **type.**

More robust than *S. callidum* (Mont.) Mitt. from which it also differs in the more glossy leaves hooked at the tips of the branches. The description of *Hypnum leucocytus* C. M. suggests something similar but Dixon remarks (Studies in the Bryology of New Zealand, Pt. VI, p. 309. 1929) that this species is not glossy while *S. aureo-nitidum* is characterized by a lustrous, almost metallic sheen.

POLYTRICHACEAE

Dendroligotrichum squamosum (Hook. f. & Wils.) Broth.

Numerous collections of this species show the end cells of the lamellae in cross section are either two-parted or single and the lamellae 4–5 cells high. The end cells have two lumens when two-parted and are scarcely suggestive of *Polytrichum commune* to which Dixon (Studies in the Bryology of New Zealand, Pt. IV, p. 235. 1926) indicates that it may have some affinity.

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THE GENUS CUNNINGHAMELLA (MUCORALES)

VICTOR M. CUTTER, JR.

The opportunity has recently arisen to examine a number of isolates of *Cunninghamella* from various localities in North America. The confused synonomy and overlapping specific descriptions available in the literature have proved most troublesome in attempting to identify these isolates. It is the author's opinion that at the present time the accurate identification of species of *Cunninghamella* is practically impossible. This situation arises in large part from the failure of earlier workers to employ a standard reproducible culture medium in their studies, and in part from the fact that the known species have not yet been studied comparatively. Our expanding knowledge of the physiology and genetics of the fungi makes it evident that in such a plastic group as the Mucorales, specific concepts can be formulated only from isolates grown on rigidly standardized media under carefully controlled conditions. Descriptions based upon field collections and gross cultures are of little value to the mycologist interested in accurate determinations. Unfortunately for the advance of mycological science, the precision of technique employed by physiologists in their studies of growth and variation in fungi has too rarely been carried over into taxonomic investigations.

METHODS

In common with most fungi, *Cunninghamella* species are very sensitive to the most minute variations in the culture medium, and the same isolate grown upon different media may present a completely different aspect. This plasticity is no less evident at changing levels of temperature and humidity. Any key to this genus can be of practical value only when the material to be identified is handled under exactly comparable conditions. Therefore the standardization of cultural techniques is imperative, and towards this end the procedure described below is suggested as a standard to be followed in the identification of species of Mucorales. It is not claimed that the medium employed represents the best possible choice for cultural studies or maintenance of mucoraceous fungi. Rather the medium is designed to be easily and inexpensively reproduced and, when formulated with CP chemicals, to be as uniform as possible. To date approximately 150 species of Mucorales have been grown upon this medium with good results in all cases.

In connection with this procedure it is understood that all cultures should originate from single spores. This is easily accomplished, in the case of *Cunninghamella*, by any of the usual techniques. The medium used in this study is designated as M.D.A. agar and is made up according to the following formula, and adjusted to pH 4.2 with 0.1 N HCl.

dextrose	40.00 gr.	thiamine chloride	0.5 mgr.
asparagine	2.00 gr.	agar flakes	15.00 gr.
KH_2PO_4	0.50 gr.	distilled water	1000.00 cc.
$MgSO_4$	0.25 gr.		

All reagents used are of CP grade. The thiamine used is Merck's synthetic, the asparagine is Bacto-Difco, and the agar is Bacto-agar flakes prepared by the Difco laboratories.

In the routine of identification, isolates are grown upon M.D.A. agar at 25° C. and 40° C. Specific descriptions are based upon material cultured at 25° C. At the 40° C. level, cultures are recorded merely as growing or not growing. Smaller intervals of temperature than these have not proved practical for the sharp delimitation of species. No attempt is made to record degrees of growth since quantitative methods are rarely practical in a taxonomic treatment, and do not lend themselves to rapid identification.

Material for microscopic examination is mounted in a solution of equal parts of phenol crystals, lactic acid, glycerin and distilled water to which a detergent, "Tergitol" Penetrant 7, is added in the ratio of 3 drops per 50 cc. of solution. To this mixture 5 percent Sudan III is added, which furnishes an easy method of distinguishing chlamydospores and hyphal bodies from conidia since the former rapidly accumulate the stain whereas the latter remain unstained. The color of conidia and other spores is determined by mounting them in water.

In connection with conidial measurements in this genus a word of caution is necessary. The shape and dimensions of conidia can not be accurately determined until they are mature and have fallen from the vesicles. *In situ* their shape is frequently obscured or distorted by crowding, in most mounts only immature conidia remain attached to the vesicles, the mature conidia being readily deciduous. Many of the aberrant measurements found in the literature as well as the statements concerning supposed differences in size and shape of the conidia of the terminal and lateral vesicles are directly attributable to the failure to recognize this fact. The term "vesicle" is used here in reference to the capitate structure terminating the conidiophores after the conidia are detached. The age of cultures determines to some degree the type of branching displayed by the conidiophores and since cultures are rarely mature until six days after inoculation, all observations are made at this time.

Under the discussion of each species the original description is reproduced, followed by an emended description of the species based upon monospore cultures grown at 25° C. on M.D.A. agar six days after inoculation. The key to species is compiled from these emended descriptions. Technical color terms cited in quotation marks are those of Ridgway (26). The accession numbers given under the heading "material examined" refer to cultures and permanent mounts filed in the author's herbarium at Cornell University.

HISTORY OF THE GENUS

The genus *Cunninghamella* was established by Matruchot (18) in 1903 upon *C. africana* collected in the French Sudan. At this time he failed to provide a generic description which was later supplied by Saccardo (30). Thaxter (36) shortly pointed out that in reality *C. africana* only represented a redescription of his *Oedocephalum echinulatum*, and that the species should therefore be known as *C. echinulata*. Matruchot had postulated that in spite of its purely conidial reproduction in the asexual phase, *Cunninghamella* should be placed in the Mucorales, and supported his claim with a series of ingenious experiments showing that *Cunninghamella* will serve as a host for species of *Piptocephalis* which are parasitic exclusively upon the Mucorales. He further indicated that the usually aseptate mycelium favored the inclusion of *Cunninghamella* in this group. His opinion was subsequently confirmed by Blakeslee (5) who discovered the zygospores of *C. echinulata* in 1904. In the following year Saito (31) described the genus *Actinocephalum* based upon *A. japonicum*. Fitzpatrick (11) has pointed out that this genus is undoubtedly synonymous with *Cunninghamella*. In 1907 Lendner (14) described *C. elegans* in Swiss soil, and later, in 1927, he (16) described *C. Blakesleeana* from North American material sent to him by Blakeslee. Stadel (32) in 1911 founded *C. Bertholletiae* upon a strain from decaying Brazil nuts, and discussed certain aspects of its growth and development upon various substrates. Shortly thereafter Bainier & Sartory (2), apparently unaware of the existence of *Cunninghamella*, erected the genus *Muratella* upon *M. elegans* collected in France. Torrey (37) showed that this species was synonymous with *Cunninghamella echinulata* Thaxter, and investigated the development and morphology of the conidia in some detail. Naumov (20), however, on the basis of its consistently spherical conidia, considered *Muratella elegans* distinct from *Cunninghamella echinulata* and erected the new combination *C. Bainieri* to include it and several of his own isolates. Ling-Young (17), on the other hand, considered *Muratella* with its curious giant conidia to be distinct from *Cunninghamella* and maintained it as a valid genus.

Paine (22) in 1927 described *C. verticillata* from the United States. This species has been reported several times subsequently, but appears to be synonymous with *C. Blakesleeana* Lendner, which had been described and published three months before. Pišpek (23) in 1929 discussed a series of isolates from Yugoslav soils and erected four new species, *C. ramosa*, *C. dalmatica*, *C. polymorpha* and *C. echinata*. None of these species has been subsequently reported and all of them seem conspecific with previously described forms, although Pišpek's meager descriptions make positive identification uncertain. In 1930, Fitzpatrick (11) briefly summarized the work on *Cunninghamella* to that date. Zycha (38) in 1935 presented the first comprehensive survey of the genus and the first key to the species. He retained the six following species: *C. microspora*, *C. albida*, *C. elegans*, *C.*

ramosa, *C. Blakesleeana* and *C. echinulata*, and presented descriptions of these compiled from the literature. All other described species were reduced by him to synonomy. This treatment has served as a standard for most subsequent work. Alcorn and Yeager (1) in 1938 published a monograph of the genus with emended specific descriptions of species collected by them in Idaho. This work contained a key to the species based in part upon the literature and in part upon their own observations, as well as numerous inaccuracies in the translations of original descriptions. While their monograph purports to cover the entire literature on *Cunninghamella*, in reality a number of species are not treated, in particular those of Pišpek and of Zycha. The latest treatment of the genus is that of Naumov (20) in 1939. He presents a descriptive key to all the known species compiled from the original descriptions and his own observations. He retains all the previously described species and erects the new combination *C. Bainieri* to include *Muratella elegans*.. He has stated that this key is only tentative and the future studies will show that many of these species are not valid.

Our knowledge of the sexuality of this genus and of the zygosporic stages is largely confined to the works of Blakeslee (6), Burger (9) and Blakeslee, Cartledge and Welch (7). The last named authors have shown that *C. elegans*, *C. Bertholletiae*, *C. Blakesleeana* and *C. echinulata* are heterothallic forms and are sexually dimorphic, a conclusion contrary to that advanced by Burger on the basis of experiments with *C. Bertholletiae*. Blakeslee (6) had previously described and figured the zygospores of *C. echinulata*, and Lendner (16) supplied the same information for *C. Blakesleeana*. The sexual stages of other described species are as yet unknown. All these authors have indicated that zygospore formation is usually initiated at temperatures above 25° C.

The systematic position of *Cunninghamella* has been treated in various ways by different authors. Matruchot (18) considered it to belong in the tribe Choanephoree in company with *Choanephora*. Lendner (15) places it in the family Chaetocladiaceae in the suborder Conidiophorae. Fitzpatrick (11), Zycha (38), Christenberry (10) and Ou (21) place it in the family Choanephoraceae, with *Blakeslea* and *Choanephora*. However, Naumov (20) creates the family Cunninghamellaceae to include *Cunninghamella*, *Thamnocephalis* and *Sigmoideomyces*. At the present state of our knowledge the latter disposition seems most natural since this group of genera forms a coherent unit well separated from *Choanephora* and *Blakeslea* by the complete absence of sporangia and the presence of echinulate globose conidia. Furthermore, the dark colored rough-walled zygospores set *Cunninghamella* apart from *Blakeslea* and *Choanephora*, which have thin-walled, smooth, more or less hyaline zygospores.

It must be pointed out in connection with the validity of the name *Cunninghamella* that this genus was founded upon the conidial or imperfect stage of *C. africana* by Matruchot in 1903. The perfect stage (i.e. the zygospores) was not discovered until 1904 by Blakeslee who described the

zygospores in *C. echinulata*. These two species are synonymous. If the strictest interpretation of the International Rules of Botanical Nomenclature is followed (i.e. Art. 57) *Cunninghamella* must be attributed to Blakeslee, who, however, failed to give a generic description with his report of the perfect stage of this fungus. On the other hand the International Rules fail to define exactly what constitutes the perfect stage of a Phycomycete of the mucoraceous type. Under proper conditions in homothallic species, and in the case of heterothallic species such as *Cunninghamella*, in the presence of two compatible strains, the gametangia and zygotes are borne upon the same mycelium which gives rise to the asexual reproductive structures. Since the perfect and imperfect stages are thus inextricably mingled it will be seen that while these fungi are pleomorphic in regard to their life cycle, there is no certain way of separating the two stages for taxonomic purposes. This situation is somewhat different from the case of certain heterothallic Ascomycetes and Basidiomycetes having pleomorphic life cycles where the perfect and imperfect stages are clearly distinguishable. Bisby (4) has pointed out other instances where the strict application of Article 57 to the Phycomycetes creates nomenclatural problems of this nature. In the Mucorales dogmatic adherence to this rule would necessitate a large number of changes in the author citations, and redescription of genera and species, because the great majority of forms have been described in their imperfect stages. Consequently in this and subsequent work on the Mucorales, Bisby's suggestions will be followed, and the first valid name applied to genus or species will stand irrespective of whether it was applied in cases where the zygotic stage was not known or described.

Cunninghamella Matruchot, Ann. Mycol. **1:** 47–50. 1903; — Saccardo, Syll. Fung. **17:** 508. 1905.
Actinocephalum Saito, Bot. Mag. Tokyo **19:** 1. 1904.
Saitomyces Ricker, Journ. Mycol. **12:** 61. 1906.
Muratella Bainier & Sartory, Bull. Soc. Mycol. France **29:** 129. 1913.

Fungi with erect or ascending conidiophores, abundant submerged sterile mycelium, aseptate when young, becoming septate in age, hyaline or light colored. Conidiophores variously branched or sometimes simple, each branch terminating in a capitate vesicle covered with minute sterigmata bearing conidia. Conidia unicellular, globose to ellipsoid, echinulate, asperulate, or smooth, deciduous. Sporangia absent. Chlamydospores occasionally present, intercalary, spherical to ellipsoid with granular or oily contents. Rhizoids present in some species at base of conidiophores or indiscriminately arranged on aerial parts. Gametangia isogamous. Zygospores globose or doliform, dark-walled, tuberculate or roughened. The known species are heterothallic and saprophytic on a wide variety of substrates.

The type species is *Cunninghamella echinulata* (Thaxter) Thaxter.

KEY TO THE SPECIES OF CUNNINGHAMELLA

1. Growing at 40° C. ..... 2.
   2. Colonies "Smoke Grey"; branches of the conidiophores sympodial, cymose or irregular, not verticillate; conidia predominantly spherical with long echinulations; giant conidia absent. .....1. **C. echinulata.**
   2. Colonies "Gull Grey," branches of the conidiophores verticillate; conidia predominantly ovoid to ellipsoid with short echinulations. ...4. **C. Bertholletiae.**
1. Not growing at 40° C. ..... 3.
   3. Giant conidia present; colonies "Smoke Grey" to "Pale Olive Buff"; conidia predominantly spherical with long echinulations or sometimes smooth. 2. **C. Bainieri.**
   3. Giant conidia absent; conidia predominantly ovoid to ellipsoid with short echinulations. ..... 4.
      4. Colonies "White"; branches of the conidiophores dichotomous, sympodial or verticillate; rhizoidal tufts apparent macroscopically; conidia up to 35 x 25 μ. 3. **C. Blakesleeana.**
      4. Colonies "Gull Grey"; branches of the conidiophores always verticillate; conidia up to 16 x 12 μ; rhizoidal tufts not apparent macroscopically. ..... 5.
         5. Chlamydospores usually present; mycelium containing much oil; habitat Brazil nuts. .....4. **C. Bertholletiae.**
         5. Chlamydospores absent; mycelium mostly lacking oil; habitat soil and seeds. 5. **C. elegans.**

1. **Cunninghamella echinulata** (Thaxter) Thaxter, Rhodora **5:** 98. 1903.
Oedocephalum echinulatum Thaxter, Bot. Gaz. **16:** 17. 1891.
Cunninghamella africana Matruchot, Ann. Mycol. **1:** 47–50. 1903.

PLATE I, A–I

"White becoming slightly yellowish. Sterile and fertile hyphae not clearly differentiated, the latter more or less irregularly and indefinitely branched. The fertile heads nearly spherical to obovoid, very variable in size, more or less distinctly areolate: maximum 45–65 μ: average 28–35 μ. Spores oval to elliptical, finely echinulate: average 10 x 12 μ; maximum 18–25 μ." — Thaxter (1891).

On M.D.A. agar:

Colonies up to 1.5 cm. high, spreading rapidly, "Smoke Grey," powdery in appearance; growing at 40° C. *Sterile mycelium* smooth-walled, much-branched, mostly aseptate, up to 20 μ in diam.; rhizoids occasional; *chlamydospores* occasional upon submerged portions, irregular in shape and size. *Conidiophores* dichotomously or cymosely, never verticillately, branched; each branch terminated in a swollen vesicle, broadly clavate to subspherical, up to 60 μ in diam., average 25–40 μ in diam.; smooth or faintly areolate, no conspicuous difference in shape of lateral and terminal vesicles. *Conidia* globose to ovoid up to 20 x 18 μ, average 11–14 μ in diam., thickly beset with very fine spines up to 4 μ in length, the immature conidia sometimes smooth. *Zygospores* described by Blakeslee (6) and not subsequently reported. Gametangia isogamous or heterogamous; zygospores nearly opaque, 46–80 x 40–63 μ, average 70 x 58 μ, thickly beset with long heavy tubercles. Zygospore formation taking place only at temperatures above 25° C.

TYPE LOCALITY: On cheese and cheesy paper, Massachusetts. Thaxter.

DISTRIBUTION: Camel dung, French Sudan, 1903, Matruchot; dried flowers, Venezuela, 1905, and Puerto Rico, 1905, horse dung, Philippines, 1905, Blakeslee; Brazil nuts and soil, (18 races), New York, 1921, Blakeslee, Cartledge & Welch; soil, Dalmatia, 1932, Johann; soil, Bastrop Co., Texas, 1932, Morrow; soil, Cuba, South Carolina, North Carolina, Louisiana, 1940, Christenberry; decaying flowers of *Cucurbita pepo*, Szechuan, China, 1940, Ou.

MATERIAL EXAMINED: Panama, C. Z., date and substrate unknown, *Weston* (Acc. no. 110); locality unknown, via Harvard Cult. Coll. (Acc. no. 127); Ontario, peas, 1941, *Groves*, (Acc. no. 152); Arnprior, Ont., peas, 1943, *Groves*, (Acc. no. 294); Ithaca, N. Y., contaminant in culture, 1943, *Cutter*, (Acc. no. 345); locality unknown, from Brazil nuts, *Blakeslee*, (Acc. nos. 374, 375); locality, date and substrate unknown, *Blakeslee*, (Acc. nos. 376, 377, 378, 379).

The type of branching is the most important character separating *C. echinulata* from the other members of this genus. The descriptions and figures of Thaxter and Matruchot indicate that they were not dealing with a form having verticillately branched conidiophores. Plate I, A, B, D, and E shows the typical cymose branching encountered in vigorous cultures. In old cultures, pseudoverticillate conidiophores may be developed through the production of secondary conidiophores on the primary conidial head. A similar situation may occur if the conidiophores are submersed, as in the example shown in Plate I, G. This is, however, an abnormality. The author does not follow Zycha (38) in considering *Muratella elegans* Bainier & Sartory, and *C. verticillata* Paine as synonyms of *C. echinulata* inasmuch as these two forms are described and figured with verticillately branched conidiophores while a study of the present material of *C. echinulata* indicates that it is remarkably constant in its cymose branching.

Some slight discrepancies exist between Matruchot's description of *C. africana* and Thaxter's description of *Oedocephalum echinulatum*, chiefly in the dimensions of the conidial heads, which in *C. africana* are said to reach 100 μ in diameter. However according to Thaxter (36) the two forms are synonymous and in general the descriptions coincide well. Naumov (20) retains *C. africana* and makes *C. echinulata* a synonym of it, which is an untenable disposition when Thaxter's opinion that *C. africana* merely constituted a redescription of his *O. echinulatum* is considered.

Alcorn & Yeager's description of *C. echinulata* contains the statement that the vesicles are areolate, an opinion which probably arises from a liberal interpretation of Thaxter's more cautious statement that the heads are sometimes faintly areolate. In the cultures studied here the areolate condition could sometimes be discerned but it certainly was not present in the majority of isolates and it was usually characteristic only of immature vesicles.

C. echinulata is the only species of *Cunninghamella* which in this study consistently showed growth at temperatures above 40° C. This characteristic, and the absence of the peculiar giant conidia described below, distinguish it clearly from the following species.

2. **Cunninghamella Bainieri** N. Naumov, Clés des Mucorinées, Paris, 1939.
Muratella elegans Bainier & Sartory, Bull. Soc. Mycol. France **29:** 9. 1913.
Muratella sp. Ling-Young, Rev. Gen. Bot. **42:** 744. 1930.

PLATE I, J–O

"Conidia all spherical 14–17 μ in diam. armed with bristles 2 μ in length; sterigmata 0.5–1.4 μ long; colonies dirty white, 1 cm. high or more; verticils of 3–8 elements, accompanied as well by longer branches of the conidiophores; swellings of 28–58 μ in diam." Naumov.

On M.D.A. agar:

Colonies 0.5–3 cm. high, "Pale Olive Buff" to "Pale Smoke Grey," powdery in appearance, not growing at 40° C. Sterile mycelium much-branched, up to 30 μ in diam., aseptate when young, in the submerged portions frequently swollen into vesicular shapes; true chlamydospores absent. Conidiophores erect, usually verticillately branched below the terminal head, sometimes with several whorls of branches, lateral branches usually less than 50 μ long. Vesicles up to 60 μ in diam., average 40 μ, lateral vesicles usually smaller than the terminals. Vesicles bearing normal conidia generally smooth, sometimes verrucose when young, vesicles bearing giant conidia markedly verrucose. *Conidia* of two sorts, predominantly spherical, sometimes broad ovoid; normal conidia hyaline 5–15 μ in diam. with slender sharp echinulations up to 3.5 μ long, giant conidia yellow to brownish, thick-walled, 15–27 μ in diam. with stout sharp echinulations up to 2 μ long or sometimes smooth, giant conidia usually borne on verrucose subterminal vesicles developing in older portions of the colony. *Zygospores* unknown.

TYPE LOCALITY: Dead wood, France, Bainier & Sartory, 1913.
DISTRIBUTION: Soil, France, 1930, Ling-Young.

MATERIAL EXAMINED: *Hibiscus* flowers, Ann Arbor, Mich., 1940, *Cutter* (Acc. no. 29); locality and substrate unknown, 1942, via American Type Cult. Coll. (Acc. nos. 348, 352, 354); locality, date and substrate unknown, C. B. S. via Blakeslee (Acc. nos. 386, 387).

This species, which is closely related to *C. echinulata*, may be easily distinguished by the presence of numerous giant conidia in older cultures, as well as by its failure to grow at 40° C. Bainier & Sartory (2) give its optimum temperature range as 25–27° C. Ling-Young (17) has discussed the morphology of the "conidies tardives" or giant conidia, of this species, and states that they are always borne upon specialized lateral heads. This contention is not strictly borne out in the material studied here where the giant conidia are frequently interspersed with smaller conidia on both terminal and lateral vesicles. However, Plate I, N shows the usual condition where these structures are confined to certain lateral vesicles. A study of Ling-Young's illustrations show that they were based upon immature conidiophores which may account for the peculiar distribution of his "conidies tardives." These structures have not been encountered in other species of *Cunninghamella*.

3. **Cunninghamella Blakesleeana** Lendner, Bull. Soc. Bot. Geneva **19:** 234. May, 1927.

Cunninghamella "A," Blakeslee, Cartledge & Welch, Bot. Gaz. **72:** 185. 1921.
Cunninghamella verticillata Paine, Mycologia **19:** 253. Sept. 1927.
Cunninghamella echinata Pišpek, Acta Bot. Inst. Univ. Zagreb. **4:** 101. 1929.

PLATE II, A–D

"Conidiophores branched, terminated by swollen heads; heads minutely verrucose, 30 μ long by 28 μ wide, bearing ellipsoid conidia with finely echinulate walls. Branches of the conidiophore verticillate or solitary, lateral branches bearing spherical, hyaline to yellow conidia; zygospores spherical to doliform, dusky black, 40 μ in diam. up to 48 μ long by 49 μ wide." Lendner.

On M.D.A. agar:

Colonies 2 to 3.5 cm. high, spreading rapidly, "White," at maturity becoming tinged with yellow and compactly matted, not growing at 40° C. *Sterile mycelium* at first dichotomous, later irregularly branched up to 20 μ in diam., aseptate, bearing prominent tufts of rhizoids or outgrowths visible macroscopically upon the aerial portions, occasionally forming vesicular swellings containing much yellow oily material upon the submerged portions; true chlamydospores lacking. *Conidiophores* erect, sometimes dichotomously or sympodially but usually verticillately branched. Lateral branches of the conidiophores variable in length and number, usually less than 50 μ long. Vesicles variable, subglobose to broadly clavate up to 65 μ in diam., average 30–40 μ in diam., lateral vesicles usually smaller than terminal vesicles, verrucose to smooth. *Conidia* hyaline, predominantly ovoid to ellipsoid with smaller subspherical conidia interspersed, up to 35 μ long x 25 μ wide, average 5–18 μ long x 4–12 μ wide, with very short widely spaced echinulations or sometimes smooth. *Zygospores* not seen.

TYPE LOCALITY: Unknown.

DISTRIBUTION: Brazil nuts purchased at many localities in eastern U. S. A. (all nuts presumably from S. America), 53 races, 1921, Blakeslee, Cartledge & Welch; soil, Iowa City, Iowa, 1927, Paine; soil, Colorado, 1930, LeClerg; soil, Grobnik, Krk Island in Adriatic Sea, 1929, Pišpek.

MATERIAL EXAMINED: Brazil nuts bought in eastern U. S. A. (all nuts presumably from S. America), 1919 (7 races) *Blakeslee* (Acc. nos. 360, 361, 362, 363, 364, 365, 366).

Cunninghamella Blakesleeana was described by Lendner (16) in 1927 with no data given concerning the substrate or locality from which it was collected beyond a brief note to the effect that the material had been forwarded to him by Blakeslee. Previously Blakeslee, Cartledge & Welch (7) had investigated and discussed the sexual condition in an undescribed species which they designated as *Cunninghamella* "A." At this time they pointed out that in many respects *Cunninghamella* "A" was intermediate between *C. echinulata* and *C. Bertholletiae*, the appearance of the colony recalling *C. echinulata*, but the aspect of the spores and conidiophores more closely approaching *C. Bertholletiae*. Lendner's description of *C. Blakesleeana* emphasized this situation, and at the start of this study it was assumed that *Cunninghamella* "A" and *C. Blakesleeana* were synonymous.

Recently in a personal communication Professor Blakeslee has informed the author that his material of *Cunninghamella* "A" did indeed constitute the type material of *C. Blakesleeana.*

The cultures studied here which were obtained from the Blakeslee collection agree well with Lendner's description except that the conidia of these isolates reach somewhat larger dimensions than those given by Lendner. It is not unusual to encounter outsize conidia up to 35 μ long. Furthermore, in this material certain outgrowths of rhizoids or sterile mycelium upon the aerial hyphae were very apparent, a feature not mentioned in Lendner's description. The presence of these rhizoidal tufts upon the mycelium in the aerial portions of the colony imparts a very characteristic appearance during the early stages of growth, and in conjunction with the pure white color of the colonies provides an easy macroscopic method of distinguishing this species from *C. elegans* and *C. Bertholletiae.*

The frequently irregular or pseudoverticillate branching of the conidiophores and the more heavily echinulate conidia are further differences between *C. Blakesleeana* and the above-mentioned species. Conidial measurements and shapes of these forms tend to overlap and do not seem reliable criteria for their separation. The data presented by Blakeslee, Cartledge & Welch based upon a study of the sexual conditions in this form and in *C. elegans* and *C. Bertholletiae* indicate that it is physiologically distinct from the latter species.

The zygospores are described by Lendner and are said to differ from those of *C. echinulata* and *C. elegans* in the shape of the segments of the epispore which are somewhat depressed or hollowed in the center, rather than flat as in *C. elegans* or tuberculate as in *C. echinulata.*

Cunninghamella verticillata Paine (22), described three months after *C. Blakesleeana*, corresponds so closely with it that it must be incorporated here. The description of *C. echinata* Pišpek fits *C. Blakesleeana* so well that it seems probable the two species are synonymous although Pišpek's description leaves much to be desired. Since *C. echinata* has never been reported subsequently and since there are no significant differences between the description of it and of *C. Blakesleeana*, Pišpek's species is here reduced to synonymy.

In common with *C. Bertholletiae*, this species occurs predominantly upon substrates with high oil or fat content, as is indicated by its repeated isolation from Brazil nuts. A detailed study of a large series of isolates from this and other substrates may reveal strains intermediate in character between this species and *C. Bertholletiae* and *C. elegans* which will necessitate the combining of this complex into one inclusive species. On the basis of our present knowledge it appears desirable to maintain them as distinct entities.

4. **Cunninghamella Bertholletiae** Stadel, Dissertation, Kiel, pp. 1–35. 1911.

PLATE II, E–G

"Colonies white, yellow to light olive, dense with interwoven mycelium, up to 2 cm. high. Conidiophores verticillately branched, the laterals sometimes showing secondary

branching. Conidiophores 9–19.2 μ thick, with heads up to 70 μ in diam., average 40–50 μ; swellings 5 x 4 μ up to 30–55 μ in diam. Conidia oval or having the form of a cucumber seed, echinulate, 16–25 x 10–12 μ, or spherical, more nearly smooth 8–9 μ in diam. Sterigmata up to 2.75 x 0.8 μ. Chlamydospores present, up to 30–40 μ in diam. Oily material usually present in mycelium, conidiophores and conidia. Species showing an affinity for oily substrates." Stadel.

Zygospores have been reported by Blakeslee, Cartledge & Welch (7) but never described.

On M.D.A. agar:

Colonies up to 2.5 cm. high, spreading rapidly, "Gull Grey," somewhat compacted, sometimes growing at 40° C.; *sterile mycelium* much branched with some spherical to ovoid chlamydospores up to 35 μ in diam. containing much oily or granular material; *conidiophores* erect, verticillately branched at some distance below the terminal heads, with as many as five whorls of lateral branches; laterals usually more than 50 μ long; vesicles subglobose to clavate, when young tuberculate or verrucose, in age becoming smooth, up to 65 μ in diam., at times filled with large oil globules; *conidia* characteristically lacrymoid, sometimes subspherical or ellipsoid, with prominent apiculus, up to 16 x 12 μ, average 9 x 7 μ, hyaline, echinulate with very short spines or asperulate; *zygospores* not seen.

TYPE LOCALITY: Nuts of *Bertholletia excelsa*, Brazil, 1911. Stadel.

DISTRIBUTION: Brazil nuts, Massachusetts, 1919, Burger; New York and localities in eastern U.S.A., 81 races (all nuts presumably collected in S. America) 1921, Blakeslee, Cartledge & Welch; soil, Moscow, Idaho, 1937, Alcorn & Yeager.

MATERIAL EXAMINED: Brazil nuts, locality unknown via American Type Cult. Coll., 1943, (Acc. nos. 95, 96, 353); via Blakeslee coll., 1943, (Acc. nos. 367, 368, 369, 370, 371, 372, 373).

Lendner (16) calls attention to the fact that this species is very close to *C. elegans*, and considers them synonymous. Zycha (38) follows this treatment, whereas Naumov (20) and Alcorn & Yeager (1) retain *C. Bertholletiae* as a specific entity. In this connection it should be recalled that Blakeslee, Cartledge & Welch (7) in their extensive work on the sexuality of *Cunninghamella* apparently experienced no difficulty in separating the two species and obtained no evidence that they were conspecific. Furthermore with the exception of Alcorn & Yeager's record, *C. Bertholletiae* has been reported only from decaying Brazil nuts while *C. elegans* is predominantly a soil inhabiting form. In the case of the race of *C. Bertholletiae* collected from Idaho soil by Alcorn & Yeager, their emended description does not coincide at all well with the original description. Furthermore their translation of Stadel's description contains certain inaccuracies which may arise from the fact that they cite as the source of this diagnosis not Stadel's own work, but only a review of it prepared by Leeke (13). Therefore the only valid evidence that the Idaho form is actually *C. Bertholletiae* is the fact that it was reputed to form zygospores when contrasted with a

minus race of this species in Blakeslee's laboratory. Under the circumstances this record must be viewed with some scepticism.

When cultured upon M.D.A. agar there are certain minor differences between the two species. *C. Bertholletiae* usually develops chlamydospores, whereas these structures are lacking in *C. elegans*. In all the material examined here the mycelium of *C. Bertholletiae* was consistently filled with granular materials or oil globules, a condition not seen in *C. elegans*. The conidia of the former are more consistently apiculate than are those of the latter, and the lateral branches of the conidiophores of *C. Bertholletiae* are on the average somewhat shorter and stouter. It must be emphasized, however, that these are not reliable criteria for the separation of the two species and are useful only in connection with a large series of isolates.

Perhaps the most significant difference between the two species is the ability of certain strains of *C. Bertholletiae* to grow at 40° C. No strains of *C. elegans* were encountered which could endure this temperature. Four of the ten cultures of *C. Bertholletiae* studied here exhibited this peculiarity. This variability between morphologically identical strains cannot be satisfactorily accounted for at the present time. However, all the cultures studied had been grown upon artificial media for a number of years before they were tested, and it is possible that during this time certain of them lost the ability to grow at higher temperature levels. While this speculation is in no sense conclusive, the temperature growth relationships of these species may prove very significant in effecting a satisfactory separation, and should be investigated in greater detail with freshly collected cultures. The only other species of *Cunninghamella* consistently able to grow at temperatures of 40° C. or higher is *C. echinulata*. In the key presented above *C. Bertholletiae* has been so placed that it may be identified in either temperature category.

In the light of the results of Blakeslee, Cartledge & Welch, and the failure in the present study to obtain zygote formation between oppositely sexed races of these two species contrasted under favorable conditions of temperature and nutrition, it seems reasonable to conclude that they are at least physiologically distinct. Consequently *C. Bertholletiae* is retained until more cogent proof of its conspecificity with *C. elegans* is presented.

5. **Cunninghamella elegans** Lendner, Bull. Herb. Boissier (II) **7:** 250–251. 1907; Les Mucorinées de la Suisse. Berne, 1908.

PLATE II, H

"Colonies white to light ashy, mycelium differentiated into two regions, the submerged region very compact, in age becoming pseudoparenchymatous and cartilaginous, the aerial portion cottony up to 2 cm. high. The conidiophores erect, branching dichotomously several times, aseptate, verticillately branched at a distance below the terminal head. Verticillate branches variable in number, terminated in heads. Terminal heads up to 60 μ in diam., lateral heads 18–20 μ in diam. Conidia of the terminal head ovoid, apiculate at point of insertion, 16 x 12–14 μ up to 14 x 22 μ, armed with very short spines. The lateral conidia smaller and more nearly spherical, 8–10 μ in diam. The conidia impart a pale ashy blue color to the colony. After dissemination of the

conidia the surface of the heads is echinulate with short tubercles, very evenly distributed, marking the points of insertion of the conidia." Lendner (1908).

Zygospores reported by Blakeslee, Cartledge & Welch (7) but never described.

On M.D.A. agar:

Colonies up to 3.5 cm. high, spreading rapidly, "Gull Grey," not growing at 40° C., in age becoming compacted. *Sterile mycelium* much branched, up to 20 μ in diam., aseptate when young, gradually becoming septate in the submerged portions, frequently forming oidia and swellings, true chlamydospores not observed. *Conidiophores* erect, verticillately branched at some distance below the terminal head; lateral branches arranged in a number of successive whorls about the primary conidiophore, laterals usually more than 50 μ long and comparatively slender. Terminal vesicles subglobose to broad clavate, up to 60 μ in diam., lateral vesicles pyriform, subglobose or clavate, up to 40 μ in diam.; vesicles for the most part very closely verrucose or tuberculate, sometimes smooth. *Conidia* hyaline, predominantly ovoid to ellipsoid, occasionally lacrymoid, up to 14–16 μ long x 10–12 μ broad, echinulate with very short spines, asperulate, or smooth. *Zygospores* not seen.

TYPE LOCALITY: Garden soil, near Geneva and Vuache, Switzerland, Lendner.

DISTRIBUTION: Soil, Cold Spring Harbor, N. Y., (42 races) 1921, Blakeslee, Cartledge & Welch; Germany, 1929, Janke; South Slavia 1929, Pišpek; Evanston, Illinois, 1929, Swift; France, 1930, Ling-Young; Bastrop Co., Texas, 1932, Morrow; Germany, 1935, Zycha; Ann Arbor, Michigan, 1914, 1917, Povah; Moscow, Idaho, 1937, Alcorn & Yeager; Canada, 1938, Bisby; North Carolina (several localities), 1940, Christenberry.

MATERIAL EXAMINED: Peas, Wellington, Ont., Arnprior, Ont., Brittania Bay, Ont., Canada, 1943, *Groves* (Acc. nos. 141, 312, 316); flaxseed, Richmond, Ont., Saskatoon, Sask., Winkler, Man., Canada, 1943, *Groves* (Acc. nos. 209, 224, 296); locality and substrate unknown, via American Type Cult. Coll. and *S. A. Waksman*, 1943 (Acc. nos. 349, 355, 357); locality and substrate unknown via Blakeslee Coll., 1943 (Acc. nos. 380, 381, 382, 383, 384, 385); parsley seed, New Haven, Conn., and Gilroy, Calif., 1942, *Groves* (Acc. nos. 388, 390); lettuce seed, Philadelphia, Pa., and San Francisco, Calif., 1942, *Groves* (Acc. nos. 389, 398); spinach seed, Toledo, Ohio, and Milford, Conn., 1942, *Groves* (Acc. nos. 395, 396); pepper seed, Toledo, Ohio, 1942, *Groves* (Acc. no. 391); pumpkin seed, Milford, Conn., 1942, *Groves* (Acc. no. 392); celery seed, Detroit, Mich., 1942, *Groves* (Acc. no. 393); muskmelon seed, New Haven, Conn., 1942, *Groves* (Acc. no. 394); carrot seed, Minneapolis, Minn., 1942, *Groves* (Acc. no. 397).

This species is common in seeds and soil throughout the temperate regions of the world. As yet no tropical records are available. The small, asperulate or shortly echinulate conidia and consistently verticillate branching of the conidiophores, with long, slender, lateral branches, make *C. elegans* easily distinguishable from all other described species except *C. Bertholletiae*. The distinguishing features of these two species have been

previously outlined. Lendner has described the peculiar vesicular swellings formed in liquid media by this species. The same phenomenon is exhibited by all isolates of *Cunninghamella* under unfavorable conditions. It must be recognized that these structures are not true chlamydospores, which in the material examined by the author occur only in *C. echinulata* and *C. Bertholletiae*. These chlamydospores are thick-walled resistant bodies, intercalary in the mycelium, while the vesicles merely represent thin-walled swollen portions of the submerged mycelium.

DOUBTFUL SPECIES

Cunninghamella albida (Saccardo) Matruchot, Ann. Mycol. **1:** 56. 1903.
Oedocephalum albidum Saccardo, Michelia **2:** 288. 1881.
Haplotrichium albidum Saccardo, Michelia **2:** 288. 1881 and Fungi Italici: fig. 805. 1881.

"Sterile mycelium repent, much branched, aseptate, hyaline. Conidiophores erect or decumbent similar to the sterile mycelium, aseptate and hyaline, simple or occasionally giving off lateral conidiophores terminated by finely muriculate vesicles. Conidia arising from the tubercles of the vesicles globose to globose elliptical (not concatenate) 2–10 μ in diam., hyaline white to pale yellow." Saccardo.

In dead and decaying roots of *Citrus Limonii* Salo, Italy, 1874.

As far as is known this species has never been collected since the original report. There seems little doubt that Saccardo was dealing with a species of *Cunninghamella* but the figure and fragmentary description given offer little possibility of future identification. Zycha and Naumov have interpreted *C. albida* as having unbranched conidiophores and use this character to separate it from other species of *Cunninghamella*. This interpretation arises from a liberal translation of the original Latin description. On the other hand, Saccardo's illustration shows a form with verticillate and dichotomously branched conidiophores, as well as several young unbranched conidiophores. Were it not for the smooth-walled conidia the species would conform well with *C. Blakesleeana*. However, in the absence of further information concerning the essential dimensions of this species, any speculation in regard to its synonymy appears unwarranted. It is therefore retained as a provisional species but not included in the key.

Actinocephalum japonicum Saito, Bot. Mag. Tokyo **19:** 1. 1904.
Saitomyces japonicus (Saito) Ricker, Journ. Mycol. **12:** 61. 1906.

"Turf grayish, mycelium irregularly branched covering the substrate; sporangiferous hyphae erect, lacking basal rhizoids, in general verticillately branched, branches terminally inflated, vesicles 25–55 μ in diam.; conidia globose or sometimes oval, 20 by 18–21 μ, inserted individually on sterigmata, hyaline, echinulate, zygospores and chlamydospores unknown." Saito.

TYPE LOCALITY: Air borne, Musashi Province, Japan.

This species placed in *Cunninghamella* by Fitzpatrick (11) and subsequently by Zycha (38) and Naumov (20), appears identical with *C. Bainieri*. Zycha and Naumov consider it synonymous with *C. elegans* Lendner, but the short verticillate lateral branches shown in Saito's illustrations and

the large finely echinulate subspherical conidia are not consistent with the concept of *C. elegans*. In the absence of the original material it will probably never be possible to determine its specific affinity.

Cunninghamella dalmatica Pišpek, Acta Bot. Inst. Univ. Zagreb. **4:** 100. 1929.

"Colonies brownish white, 1 cm. high, conidiophores mostly verticillately branched immediately below the apex, terminal heads 28–52.5–56 μ in diam., lightly verrucose; lateral heads 14–24.5 μ diam.; conidia globose 7–8 μ diam. to ovoid 7–14 μ long by 7–10.5 μ wide." Pišpek.

TYPE LOCALITY: Cultivated soil near Jesenice, Dalmatia.

MATERIAL EXAMINED: Locality, date, and substrate unknown, C.B.S. via Blakeslee (Acc. no. 386).

The incomplete description given by Pišpek will not allow this species to be positively identified. The culture received under this designation from Professor Blakeslee's collection is believed to represent a subculture of Pišpek's type. Upon examination it proved identical with *C. Bainieri*. This cannot be accepted as conclusive evidence that these two forms are synonymous because of the possibility of contamination during transfer of the cultures. On this basis, and because of the incomplete diagnosis furnished by Pišpek, there is no justification for maintaining *C. dalmatica* as a valid species.

Cunninghamella ramosa Pišpek, Acta Bot. Inst. Univ. Zagreb. **4:** 102. 1929.

"Colonies yellow-brown, 2 cm. high, externally resembling certain Absideae. Conidiophores in the middle of the culture for the most part simply branched, frequently inflated at the base, those on the outer periphery of the culture abundantly sympodially or irregularly branched; terminal heads for the most part verrucose 42–59–77 μ in diam.; lateral heads 14–38 μ wide; spores mostly globose, very large, yellowish, granular within, not echinulate, 10.5–24.5–35 μ in diam. or globose and pyramidal, 10.5–14 μ long by 7–9–10.5 μ wide; chlamydospores not seen, zygospores unknown." Pišpek.

TYPE LOCALITY: Rich pasture soil near Kraljevo (Serbia occid.).

On the basis of Pišpek's description this species appears closely related to *C. Bainieri*. The only significant differences are the irregular branching of *C. ramosa* and its predominantly smooth-walled conidia. However, Plate I, M shows an irregularly branched conidiophore of *C. Bainieri* and smooth-walled giant conidia are not infrequently found in this species. The large dimensions of the conidia of Pišpek's isolate certainly indicate a close connection with *C. Bainieri*. This species has never been reported subsequently, and until more information can be accumulated its validity must be questioned.

Cunninghamella polymorpha Pišpek, Acta Bot. Inst. Univ. Zagreb. **4:** 103. 1929.

"Colonies brownish white, dense, 2 cm. high, conidiophores very diversely branched; terminal heads verrucose, 32–49–55 μ in diam.; lateral heads 10.5–17.5–25 μ in diam.; spores globose 7–14–(17.5) μ in diam., or ovoid to ellipsoidal 7–10.5–(14) μ wide by 7–10–(17) μ long, hyaline or yellowish; chlamydospores not seen, zygospores unknown." Pišpek.

TYPE LOCALITY: Soil between rocks on Mt. Puvarov, elevation 1300 metres, Croatia.

MATERIAL EXAMINED: Locality, date, and substrate unknown. C.B.S. via Blakeslee (Acc. no. 387).

The isolate of this species received from Professor Blakeslee's collection was identical with isolates of *C. Bainieri*. The description furnished by Pišpek indicates that the measurements of his type isolate overlap those of *C. dalmatica*, and he presents no significant data which will permit the separation of these two species. On the basis of his description positive identification of *C. polymorpha* is impossible.

EXCLUDED SPECIES

Cunninghamella microspora (Riv.) Matruchot, Ann. Mycol. **1:** 56. 1903.
Gonatobotrys microspora Rivolta, Dei Parassiti Vegetali, p. 490. Torino, 1873.
Prachtflorella microspora (Riv.) Matruchot, Ann. Mycol. **1:** 56. 1903.

This species, placed in *Cunninghamella* by Matruchot, has been incorporated in the genus by all subsequent authors, although as far as can be determined it has been reported only by Rivolta in 1873 and by Berlese in 1889. Rivolta's description consists of the single line "La Gonatob. microspora. — Ha le spore piccolissime.", and the single figure given is too fragmentary to give any real concept of the species. Knowledge of the form is therefore confined to the descriptions and figures presented by Berlese from material encountered on dead and decaying bark of *Morus alba* in Northern Italy. A perusal of this description shows this species to be quite different from any of the forms discussed above. The restricted nature of the colony, the extremely small dimensions of the mycelium (2–3 μ in diam.), and particularly the presence of unbranched conidiophores with intercalary spore-bearing nodes are characters not associated with the original concept of *Cunninghamella* as outlined by Thaxter and Matruchot. Furthermore, the elongate, basally apiculate, smooth conidia do not correspond well with the usual conidial type in *Cunninghamella*. Matruchot's comments on the relationships of *C. microspora* and his proposal of the alternate name *Prachtflorella microspora* indicate that his disposition of it was provisional, and subsequent studies have not yet confirmed his opinion. In the absence of any knowledge of the sexual stage of this species it seems advisable to exclude it from *Cunninghamella*.

Cunninghamella mandshurica Saito & Naganishi, Bot. Mag. Tokyo **39:** 285. 1913.

This species has been shown to belong in *Choanephora* by Fitzpatrick (11). The longitudinally striate conidia exclude it from *Cunninghamella*, although the type of branching is in some respects intermediate between the two genera. Zycha (38) considers the species synonymous with *Choanephora cucurbitarum*.

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The author wishes to extend special thanks to Dr. J. Walton Groves of the Canadian Department of Agriculture for the contribution of a large series of cultures which made possible this study. Acknowledgment is also made to Dr. D. H. Linder and Dr. W. L. White of the Farlow Herbarium, Harvard University, and Dr. S. A. Waksman who have contributed cultures and made many helpful suggestions. The curators of the American Type Culture Collection have most generously cooperated by making available all cultures of *Cunninghamella* in their collection. Dr. Kenneth Raper has extended valuable aid by donating many cultures from the Blakeslee Collection. Finally the author wishes to acknowledge the aid of Miss Shirley Weinstein, who assisted in the cultural studies of this material.

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BIBLIOGRAPHY

1. **Alcorn, G. D., & C. C. Yeager.** A monograph of the genus *Cunninghamella*, with additional descriptions of several common species. Mycologia **30:** 653–658. 1938.
2. **Bainier, G., & A. Sartory.** Etudes morphologique et biologique du *Muratella elegans* n. sp. Bull. Soc. Mycol. France **29:** 129–136. 1913.
3. **Berlese, A. N.** Fungi Moricolae. Padova, 1889.
4. **Bisby, G. R.** Who is the author? Trans. British Mycol. Soc. **25:** 434–435. 1942.
5. **Blakeslee, A. F.** Sexual reproduction in the Mucorineae. Proc. Amer. Acad. Arts and Sci. **40:** 205–319. 1904.
6. ————. Two conidia-bearing fungi. *Cunninghamella* and *Thamnocephalis*, n. gen. Bot. Gaz. **40:** 161–170. 1905.
7. **Blakeslee, A. F., J. L. Cartledge & D. S. Welch.** Sexual dimorphism in *Cunninghamella*. Bot. Gaz. **72:** 185–219. 1921.
8. **Briquet, J.** International Rules of Botanical Nomenclature. Jena, 1935.
9. **Burger, O. F.** Sexuality in *Cunninghamella*. Bot. Gaz. **68:** 134–146. 1919.
10. **Christenberry, G. A.** A taxonomic study of the Mucorales in the southeastern United States. Journ. Elisha Mitchell Sci. Soc. **56:** 333–366. 1940.
11. **Fitzpatrick, H. M.** The Lower Fungi; Phycomycetes. New York, 1930.
12. **LeClerg, E. L.** Cultural studies of some soil fungi. Mycologia **22:** 186–210. 1930.
13. **Leeke, N.** Review of, Stadel, O. Über einen Neuen Pilz *Cunninghamella Bertholletiae*. Dissert. Kiel, 1911. Mycol. Centralbl. **1:** 218–219. 1912.
14. **Lendner, A.** Sur quelques Mucorinées. Bull. Herb. Boissier. ser. II, **7:** 250–251. 1907.
15. ————. Les Mucorinées de la Suisse. Berne, 1908.
16. ————. Une nouvelle espèce de Mucorinée, le *Cunninghamella Blakesleeana* Lendner. Bull. Soc. Bot. Geneva **19:** 234–238. 1927.
17. **Ling-Young, M.** Étude biologique des phénomènes de la sexualité chez les Mucorinées. Rev. Gen. Bot. **42:** 722–752. 1930.
18. **Matruchot, L.** Une Mucorinée purement conidienne, *Cunninghamella africana*. Ann. Mycol. **1:** 45–60. 1903.
19. **Morrow, M. B.** The soil flora of a pine forest. Mycologia **24:** 398–402. 1932.
20. **Naumov, N. A.** Clés des Mucorinées. Paris, 1939.

21. **Ou, S. K.** Phycomycetes of China I. Sinensia **2:** 427–449. 1941.

22. **Paine, F. S.** Studies of the fungous flora of virgin soils. Mycologia **19:** 248–267. 1927.

23. **Pišpek, P. A.** Edafske mukorinje Jugoslavije. Acta Bot. Inst. Bot. Univ. Zagreb. **4:** 77–112. 1929.

24. **Povah, A. H. W.** *Helicostylum* and *Cunninghamella:* two genera of the Mucorales new to the state. Ann. Rept. Mich. Acad. Sci. **17:** 152–155. 1915.

25. **Ricker, P. L.** Second supplement to new genera of fungi published since the year 1900, with citation and original descriptions. Journ. Mycol. **12:** 60–67. 1906.

26. **Ridgway, R.** Color Standards and Nomenclature. Wash., D. C. 1912.

27. **Rivolta, S.** Dei Parassiti Vegetali. Torino, 1873.

28. **Saccardo, P. A.** Fungi veneti novi vel critici v. mycologiae venetae addendi. Series XII. Michelia **2:** 241–301. 1881.

29. ————. Fungi Italici Autographice Delineati. fig. 805. Patavii, 1877–1886.

30. ————. Syll. Fung. **17:** 508. 1905.

31. **Saito, K.** *Actinocephalum japonicum* nov. gen. et nov. spec. Bot. Mag. Tokyo **19:** 36–38. 1905.

32. **Saito, K. & H. Naganishi.** Eine Neue Art von *Cunninghamella.* Bot. Mag. Tokyo **29:** 285–286. 1915.

33. **Stadel, O.** Über einen neuen Pilz, *Cunninghamella Bertholletiae.* Dissert. Kiel. 1–35. 1911.

34. **Swift, M. E.** Contributions to a mycological flora of local soils. Mycologia **21:** 204–221. 1929.

35. **Thaxter, R.** On certain new or peculiar North American Hyphomycetes. I. *Oedocephalum, Rhopalomyces* and *Sigmoideomyces* n. g. Bot. Gaz. **16:** 14–26. 1891.

36. ————. A New England Choanephora. Rhodora **5:** 97–102. 1903.

37. **Torrey, G. S.** Les Conidies de *Cunninghamella echinulata* Thaxter. Bull. Soc. Mycol. France **37:** 93–99. 1921.

38. **Zycha, H.** Kryptogamenflora der Mark Brandenburg, Pilze II, Mucorineae: 1–264. Leipzig, 1935.

EXPLANATION OF PLATE I.

All figures drawn with the aid of a camera lucida at a magnification of x1300 and reduced in printing to an approximate magnification of x325.

A–F. *Cunninghamella echinulata.* Types of conidiophores and conidia produced on M.D.A. agar.

G. *Cunninghamella echinulata.* Conidiophore and conidia produced on liquid medium, showing attenuated lateral branches and long echinulations on conidia.

H–I. *Cunninghamella echinulata.* Vesicles and chlamydospores formed on submerged mycelium.

J–M. *Cunninghamella Bainieri.* Types of conidiophores and conidia.

N. *Cunninghamella Bainieri.* Conidiophore showing arrangement of giant conidia on specialized lateral branch.

O. *Cunninghamella Bainieri.* Types of conidia.

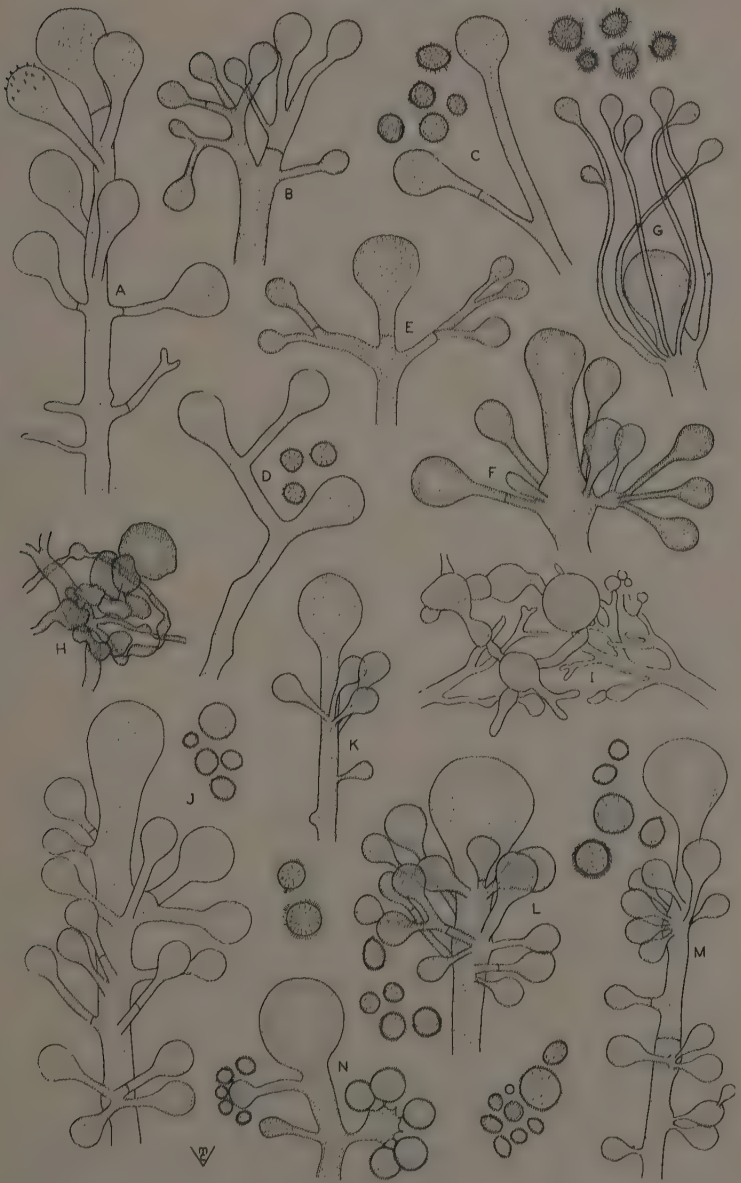

PLATE I

EXPLANATION OF PLATE II.

All figures drawn with the aid of a camera lucida at a magnification of x1300 and reduced in printing to an approximate magnification of x325.

A–D. *Cunninghamella Blakesleeana*. Types of conidiophores and conidia.

E–G. *Cunninghamella Bertholletiae*. Types of conidiophores and conidia.

H. *Cunninghamella elegans*. Conidiophore and conidia.

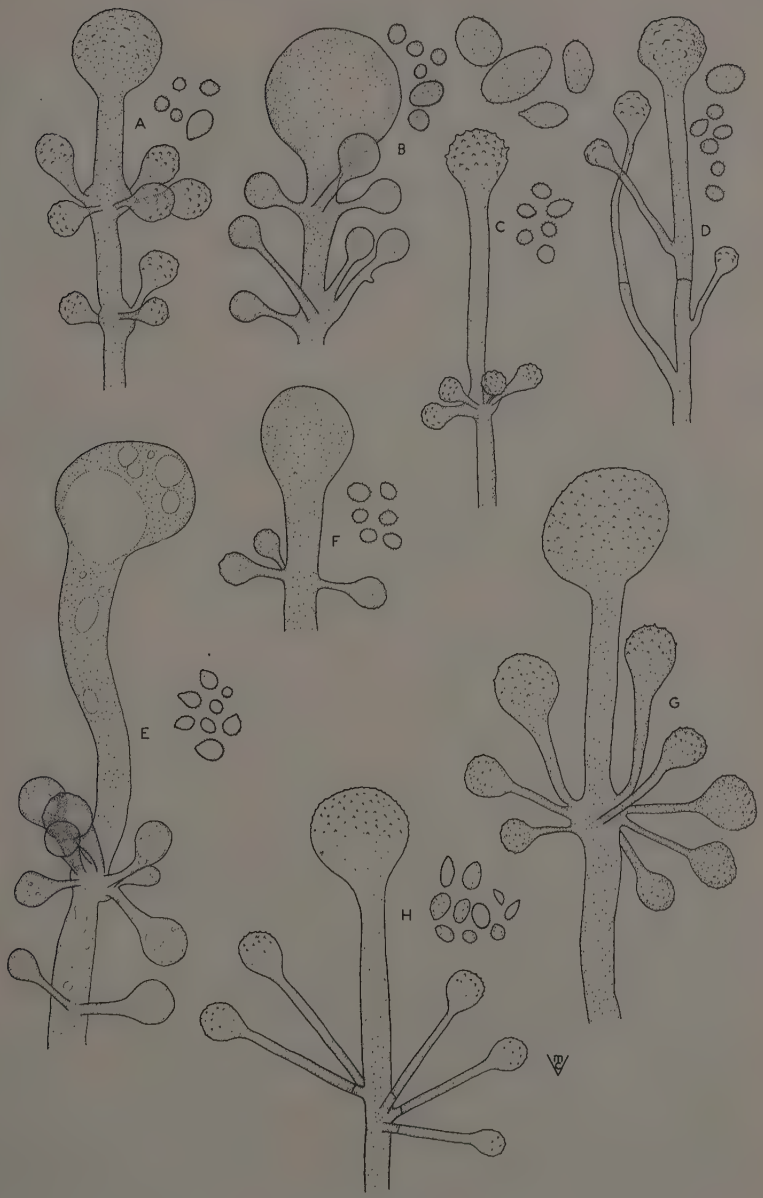

PLATE II

2(3):345–383 FARLOWIA JANUARY, 1946

A COMPARATIVE STUDY OF TORULOPSIS PULCHERRIMA AND TAPHRINA DEFORMANS IN CULTURE [1]

CATHERINE ROBERTS

INTRODUCTION

The concept of a morphologic or phylogenetic relationship existing between the yeasts and the fungi comprising the order Taphrinales (or Exoascales) is not of recent origin. Reess (1870), De Bary (1884), and Hansen (1904) all expressed such an opinion, based upon macroscopic and microscopic resemblances in culture between the two groups of fungi. At present, two widely used schemes of mycological classification, that of Gäumann and Dodge (1928) and that of Bessey (1935, 1942), differ radically in regard to the relative positions of the Taphrinales and the yeasts. From a phylogenetic point of view, Gäumann and Dodge place the two groups in the primitively simple Hemiascomycetes, but separate the yeasts from the Taphrinales by relegating the former to the order Endomycetales. On the other hand, Bessey regards the yeasts and the Taphrinales as being widely separated, the latter representing an offshoot of the Pezizales (which he assumes to be primitive), while the yeasts are regarded as "the ultimate degree of simplification in the Class Ascomyceteae" and are therefore placed at the end of this group. In 1937 Guilliermond concluded that ". . . les Exoascées que la plupart des mycologues modernes s'accordaient à séparer radialement des levures et à rattacher aux Ascomycètes supérieurs . . . nous apparaissent, au contraire, beaucoup plus proches des levures qu'on ne le pensait et l'on en revint ainsi aux anciennes conceptions de Reess, de Bary et Hansen."

These concepts were based on similarities evident in culture, but it should be emphasized that only one phase in the life cycle of *Taphrina* — the saprophytic, budding stage — has been found to be readily capable of development on artificial media. The parasitic, mycelial stage of this genus, involving sexuality, has resisted all attempts at culture, exclusive of scattered reports in the literature to be referred to later in more detail.

In brief, the life cycle of *Taphrina deformans* (Berk.) Tul., the causal agent of peach leaf curl and the species investigated in this study, is as follows: Asci are formed in the spring and summer on the surfaces of infected leaves, and each normally produces eight haploid ascospores which are discharged in a group. The ascospores fall to various parts of the host plant and initiate a yeast-like budding or sprout conidial stage, in which

[1] Portion of a thesis submitted to the Graduate Division, University of California in partial satisfaction for the degree of Doctor of Philosophy, October, 1943. The valuable advice and criticisms offered during the course of the investigation and in the preparation of the manuscript by Prof. J. T. Barrett, Dr. H. N. Hansen, Dr. E. M. Mrak, and Prof. M. W. Gardner are gratefully acknowledged.

form the organism overwinters. In the following spring when the leaf buds are expanding, infection occurs through penetration by an infection hypha produced by germination of the sprout conidium. It is believed (Eftimiu 1927, Fitzpatrick 1934, Martin 1940) that the occurrence of nuclear division without cross-wall formation in this germinating cell is responsible for the origin of the binucleate or dicaryon condition which is evident in the cells of the intercellular mycelium subsequently developing throughout the leaf tissue. From this mycelium is formed a subcuticular layer of rather thick-walled binucleate cells, the ascogenous cells. Karyogamy occurs in these, followed by the extrusion of the cell wall to form the ascus, which in its development ruptures the cuticle. The diploid fusion nucleus divides mitotically, one of the daughter nuclei passing into the ascus, which is then cut off from the ascogenous cell by a cross wall. Meiotic and mitotic nuclear divisions then occur, resulting in the formation of eight haploid ascospores, and the cycle is completed. In investigations of other species of *Taphrina* by Wieben (1927) the origin of the dicaryon was reported to occur through the copulation of physiologically differentiated ascospores or their derivatives, but in *T. deformans* only rare instances of copulation have been noted (Mix 1929), and it is generally believed that this species is homothallic.

As a group, the yeasts are readily culturable and may be maintained for long periods of time on various types of artificial media, both natural and synthetic. The majority of the yeasts are saprophytic organisms, but parasitic forms exist, both on plants and animals. Yeasts fall into two main groups — the sporogenous or sporulating and the asporogenous or non-sporulating forms. The sporulating yeasts pass through complete life cycles in culture, and although the types of sexuality involved are greatly diversified, the formation of ascospores within asci at some stage in development is a constant occurrence in all those organisms investigated. Those yeasts which have never been known to produce spores in culture are known as the imperfect yeasts and have been regarded by some as perfect yeasts which have lost their sporulating ability. They are placed among the Fungi Imperfecti, and, as would be expected, no attempt to relate them one to another in a natural system is made, but they are merely classified for convenience in identification. Their development in culture lacks any type of sexuality or alternation of haploid and diploid generations and consists merely of a predominantly budding type of vegetative reproduction, which often exhibits a pseudomycelial tendency. The genus *Torulopsis* is classified with the imperfect yeasts in the family Torulopsidaceae and the sub-family Torulopsidoideae, the latter being characterized by the absence of pseudomycelium, or, if present, by a very primitive type (Lodder 1934).

An important contribution to our knowledge of the imperfect yeasts was made by Lodder in 1934. As a result of a detailed study of the physiology and morphology of these organisms (exclusive of the pseudomycelial-forming Mycotoruloideae), she erected a scheme of generic and specific determination which has since been recognized as the standard scheme of

classification for these non-sporulating forms. From the standpoint of the problem of the relationship between the yeasts and the Taphrinales, this work is significant because of the fact that if this key is used, the genus *Taphrina*, as represented by its saprophytic budding stage in culture, will fall into the genus *Torulopsis*. The importance of this can hardly be overemphasized, for it is possible, therefore, that isolates of *Taphrina* may be identified as belonging to the genus *Torulopsis*. The differences in the natural habitats of these two groups of fungi are not so great as to preclude their being isolated from similar or identical material, for, although the budding stages of the parasitic species of *Taphrina* are quite closely associated with their hosts, the species of *Torulopsis* are quite widespread and have been isolated from a great variety of living and non-living material. In this connection, the investigations of Koch (1934) on the overwintering of parasitic and saprophytic fungi on fruit trees stress the actual difficulty involved in the identification of isolates of *Taphrina deformans*. Koch states, "Among numerous other fungi appearing in isolations from buds and bark of *Prunus persica*, an organism resembling *Taphrina deformans* appeared on five occasions . . . as this organism is somewhat difficult to distinguish from certain 'budding' saprophytic fungi, many of which appear consistently in isolations from the bark of peach trees, it was necessary to prove the identity of the organism by inoculation."

Studies of the general cultural behaviour of species of *Taphrina* have already been referred to, but some recent investigations of *Torulopsis* spp. in culture are worthy of mention at this time. Punkari and Henrici (1933, 1935), through the employment of single cell technique, studied the cultural variation occurring in several generations of *Torulopsis pulcherrima* (Lindner) Saccardo and noted striking dissociation into pigmented and non-pigmented colonial areas. The white variants, although showing a tendency to "breed true," were never completely stable, and the authors concluded that these phenomena could be explained by the occurrence of "mutation-like changes" which, in a few cases, appeared to be reversible. Three years later, Porchet (1938), although apparently unaware of Punkari and Henrici's contributions, also reported the occurrence of dissociation in *T. pulcherrima*. Her results, based upon mass transfer technique, indicated that the formation of the pigmented and non-pigmented types may be a reversible phenomenon. In 1936 there appeared a paper by Todd and Herrmann dealing with the life cycle of a yeast which is known as the causal agent of yeast meningitis. This organism had been known as *Torula histolytica* Stoddard and Cutler until Lodder (1934), considering the generic name *Torula* Turpin to be invalid, designated it as *Torulopsis neoformans* (Sanfelice) Lodder. Todd and Herrmann, however, on the basis of priority, adopted the name *Cryptococcus hominis* Vuillemin and described the occurrence of heterogamous copulation and the formation of single-spored, thick-walled asci in this organism. This constituted the first report of sporulation in the genus *Torulopsis*. Because of the transformation of the zygote into the ascus, and the formation of only one ascospore per ascus,

Todd and Herrmann designated the perfect stage of *C. hominis* as *Debaryomyces hominis* (Vuillemin) Todd and Herrmann. A complete life cycle was then formulated for this species, but it should be pointed out that it was based on isolated observations of various types of morphological structures, the actual sequence of events in the developmental life cycle of individual cells not having been observed. Confirmation of Todd and Herrmann's observations on the formation of single spores in this yeast was reported by Giordano (1938–39) and Henrici (1941), the latter also citing a paper by Redaelli, Ciferri, and Giordano (1937) in which sporulation was described.

In 1938 Windisch described for the first time heterogamous copulation and subsequent ascospore formation in *Torulopsis pulcherrima*, apparently occurring in response to the effect of a *Penicillium* contaminant in the cultures. In this organism, four spores were produced per ascus.

Two years later Windisch (1940) in a lengthy paper supplemented by drawings and photomicrographs described in detail the life cycle of *T. pulcherrima* (in pure culture) with particular emphasis laid upon the method of sporulation. In addition, observations were made upon another imperfect yeast, *Candida tropicalis* (Castellani) Berkhout [2] and a discussion of the relationship of these fungi to each other and to the Taphrinales was included. Through actual observation of the developmental sequence of individual cells in hanging drop cultures, Windisch was able to formulate a life cycle for *T. pulcherrima* which, in brief, is as follows: Large thick-walled cells containing large oil droplets (typical "pulcherrima cells") which were interpreted as ascus mother cells (ascogenous cells) occurred in old cultures; these gave rise to bud-like protrusions into which passed a portion of the oil droplet and in which were subsequently formed four ascospores; rupture of the wall of this protrusion (or ascus) liberated the spores, the empty ascus wall remaining attached to the ascus mother cell; copulation occurred between cells derived from germination of the ascospores and resulted in the subsequent formation of large thick-walled "pulcherrima cells." Nuclear staining revealed a binucleate condition in all vegetative cells as well as in the ascus mother cells. These phenomena, which were also similar to those of *Candida tropicalis*, were interpreted by Windisch as being indicative of a definite relationship with the Taphrinales. He therefore proposed that *T. pulcherrima* be incorporated in the genus *Candida* as *C. pulcherrima* and "alle candidoiden Pilze mit gleichartigen Entwicklungsgängen zusammenzufassen in der neuen Familie der Candidaceae, die in der Ordnung der Exoascales einzureihen wäre."

It should be noted that these proposals of Windisch were based upon a comparison of the cultural behaviour of *T. pulcherrima* with previous descriptions in the literature of the culturable as well as the parasitic stages of *Taphrina*, especially those of Wieben on the heterothallic species, *T.*

[2] The genus *Candida* is placed in the family Torulopsidaceae but because of abundant production of pseudomycelium is included in the sub-family Mycotoruloideae, rather than with *Torulopsis* in the Torulopsidoideae (Lodder 1934).

epiphylla Sadeb. and *T. klebahni* Wieben. Windisch made no comparative studies on the behaviour of *Taphrina* spp. in culture.

In the present investigation, a study of the comparative cultural behaviour of one isolate of *T. pulcherrima* and several isolates of *T. deformans* was made in order to obtain additional information which could be used either in substantiation or rejection of the proposals of Windisch in regard to the relationship between *T. pulcherrima* and the genus *Taphrina*. *T. deformans* was chosen for this purpose because its economic importance has attracted the attention of a large number of investigators, whose cumulative efforts have resulted in this species having become the best known representative of the Taphrinales. It is, of course, obvious that a comparative study of any two species based upon observations of only one or a few isolates from each will not give a complete picture of the range of existing differences or resemblances. The present results, therefore, are considered of necessity only preliminary, but it is hoped that they may be used as a basis for future comparative studies of these or similar organisms.

MATERIALS AND METHODS

SOURCES OF CULTURES

The strain of *Torulopsis pulcherrima* used in this investigation was kindly supplied by Dr. E. M. Mrak of the Division of Fruit Products, University of California, and had been isolated by him from the surfaces of ripe Concord grapes obtained in Walnut Creek, California. This particular isolate had been maintained in culture for several years prior to the present investigation.

Isolates of *Taphrina deformans* were secured from infected leaves of peach trees growing on the Berkeley campus and in Piedmont in April and May, 1941, and in the Kirkman Nurseries in Bethany, California, in April, 1942. The peach trees from which isolations were made consisted of ornamental types of unknown variety as well as the commercial varieties, Yunnan and Shalil.

The usual method of obtaining *Taphrina* spp. in culture was employed (Martin 1925, Mix 1935). This consisted of attaching, by means of melted wax, fragments of infected leaves containing actively discharging asci to the underside of a Petri dish cover which was then placed over the lower half containing solidified agar. Ascospores in groups of eight were subsequently discharged upon the agar surface, and when transferred to agar slants, each individual group budded readily, producing a colony which represented a single ascus culture. In obtaining single spore cultures of *T. deformans*, the eight ascospores derived from a single ascus were separated one from another by means of a micromanipulator which is described below.

STOCK MEDIA

The cultures of both *T. deformans* and *T. pulcherrima* were maintained, for the most part, at room temperature (20°–25° C.) on potato dextrose

agar with a pH range from 5.6 to 6.0. In addition, the vegetable agar of Mrak, Phaff, and Douglas (1942) which consists of equal parts of carrots, beets, cucumbers, and potatoes with 2% agar at a pH of ca. 5.7 was employed. Limited use was made of a medium composed of a juice extraction from leaves of susceptible peach varieties, with the addition of 2% dextrose and 2% agar. Liquid media were not used for maintaining stock cultures.

SINGLE CELL TECHNIQUE

All single cell isolations of both organisms were carried out by means of a locally made micromanipulator attached to the stage of a Leitz compound binocular microscope. A single glass needle, the tip of which varied from about 10 to 17 μ in diameter, was clamped in the holder of the micromanipulator in such a position that its tip was between the low power objective and the object in focus, at a magnification of 100x. Three different motions of the needle in two planes were made possible by three screw adjustments. The culture to be used was streaked across a plate of potato dextrose agar and incubated at room temperature. When growth was evident macroscopically, a block of agar, 10 to 15 mm. square and containing on one edge a portion of the margin of the streak, was cut out and transferred to a sterile slide. This was placed under the low power objective of the miscroscope, and the margin of the colony and the tip of the glass needle were brought into focus. By moving the needle, a single cell at the margin was then separated from the colony by being drawn or pushed along the surface of the agar. Plate I, Fig. 1 shows a single cell separated in such a manner from the margin of a colony of *T. deformans*. After the cell had been moved to a distance of 2 to 5 mm. from the colony, its position on the agar block was designated by making an indentation in the agar around the cell by means of the tip of the needle. Four or five isolations were made on each agar block, which was then placed in a sterile moist chamber, and after one to seven days, depending upon the growth rate of the organism, a small colony derived from the single cell was usually evident under the dissecting microscope (Plate I, Fig. 2). Transfers were accomplished by touching the colony with the tip of a sterile needle and transferring the adhering cells to an agar slant. It was found possible, after some practice, to make twenty-five to thirty single cell isolations with the micromanipulator in an hour. The dilution plate method of isolating single spores as described by Hansen and Smith (1932), although possessing the advantage of greater rapidity, was not satisfactory for the fungi studied because of the comparatively small size of the cells which did not permit them to be easily distinguished under the dissecting microscope from numerous particles apparent in the agar. A definite advantage of the micromanipulator method over the dilution plate method is that the use of the compound microscope with its higher magnification made possible the isolation of any individual cell desired, as well as its positive identification as a thin-walled cell, a thick-walled cell, a rod-shaped cell, etc. A similar technique was used to obtain monosporous cultures of *T. deformans* from dis-

charged groups of eight ascospores, only that here the ascospores were separated one from another by drawing them out with the micromanipulator needle in radial directions from the center of the group.

STAINING METHODS

Most of the observations on cellular morphology were made from unstained living material in water mounts. In a few instances, a stain of cotton blue in lactophenol was used (Rawlins 1933), a .025% solution being found the most satisfactory.

For demonstrating the nuclei in the cells of *T. pulcherrima*, Laustsen's modification of the Feulgen technique (Winge 1935) gave fairly satisfactory results, as had previously been noted by Windisch (1940) for the same organism. The method consists of smearing the organism on a clean slide by means of a cover slip, immersing in chloroform for thirty seconds, immersing in cold water for two minutes, hydrolyzing in 1N–HCl at 60° C. for five to fifteen minutes, washing in water, and staining in alcoholic fuchsin for three hours. This method was not found to be satisfactory as a nuclear stain for the cells of *T. deformans*. The iron-alum-haematoxylin schedule of Rawlins (1933) gave only fair results, while the use of Mayer's haem-alum (Chamberlain 1932) was somewhat more satisfactory. This latter method consisted of smearing the organism on a clean slide which had been coated with a thin film of albumin, fixing in formalin-acetic-alcohol No. 2 (Rawlins 1933), washing in water, staining in Mayer's haem-alum overnight, and counterstaining with either erythrosin or eosin for one-half minute.

PHYSIOLOGICAL TESTS

The comparatively few physiological tests undertaken were performed in accordance with the methods described by Lodder (1934) in her monograph on the imperfect yeasts for the determination of fermentative ability, the determination of sugar assimilation by non-fermenting strains, and the determination of nitrogen utilization.

PHOTOGRAPHY

The majority of photomicrographs were taken with a Zeiss Contax camera with a Miflex attachment. In printing, the microfilms were enlarged 2x.

EXPERIMENTAL RESULTS AND THEIR INTERPRETATION

MACROSCOPIC VARIATION IN CULTURE

The general appearance of the growth of *T. deformans* on potato dextrose agar showed a striking resemblance to that of *T. pulcherrima* on the same medium. Colonies of both organisms may be characterized by the phrase "yeast-like growth," which, although not specific, is nevertheless frequently employed as a descriptive term for the budding stages of various unrelated fungi.

After several weeks at room temperature on potato dextrose agar both *T. deformans* and *T. pulcherrima* produced colonies which were smooth, dull (sometimes slightly glistening), dry, slightly convex, and with predominantly entire borders. The most important distinguishing character between the appearance of the two fungi in culture was in the pigment formation. Although both organisms normally develop reddish or pinkish pigment of a non-carotinoid nature (Lodder 1934), that of *T. deformans* is non-diffusible, while that of *T. pulcherrima* readily diffuses into the surrounding medium. In addition to the diffusibility of the pigment, the two organisms were also distinguished by the actual color of the pigments produced. The pinkish color of the normal colonies of *T. deformans* was identified as pale grayish vinaceous by using Ridgway's color standards (1912), but sectors of greater or lesser intensity of color frequently occurred. The normal colonies of *T. pulcherrima* produced varying shades of red, characterized according to Ridgway as vinaceous russet, avellaneous, sorghum brown, and army brown. In the unpublished description of this strain made at the time of isolation, E. M. Mrak had characterized the colony color as "pale pinkish buff" on wort agar, while Mix (1924) had described the appearance of colonies of *T. deformans* on potato dextrose agar as "moist" and "shining" and their color as "pale vinaceous pink."

The occurrence of cultural variation in the form of sectors was very frequent in mass and single cell colonies of these organisms, and in addition to the colors described above, *T. deformans* frequently produced mustard or Naples yellow sectors as well as white or non-pigmented sectors which darkened with age. *T. pulcherrima* likewise produced abundant non-pigmented sectors which darkened with age to colors characterized as Tilleul-buff and vinaceous buff. Thus, the usage of the term "non-pigmented" as descriptive of white colonies or sectors for comparison with red pigmented colonies is not a completely accurate one, for the white areas may darken with age to shades of pale brown or buff. Likewise, the term "red" is used with reservations, for no distinction is made among the previously described varying shades of red developing in old cultures with diffusible pigment.

Although smoothness appeared to be a normal character of the surface of colonies, both young and old cultures of *T. deformans* at times produced roughened areas, some of which were in the form of sectors. These areas, usually of the papillate type, were found to develop sporadically and seemingly bore no relation to the colony color. Rough surfaces, both papillate and crateriform, were also found in cultures of *T. pulcherrima* but were usually confined to non-pigmented cultures which had darkened with age. The papillate type was much more common in this organism than was the crateriform.

These preliminary observations demonstrated the close resemblance between the cultural appearance of *T. deformans* and *T. pulcherrima*, suggesting the possibility of confusion in identification, especially if Lodder's recent generic key for the determination of the non-sporulating yeasts

is used. Differentiation of the genera on the basis of a diffusible pigment is, of course, possible, but because of the production in culture of non-pigmented variants of both organisms, such types may be isolated directly from nature.

ANALYSIS OF SINGLE SPORE CULTURES OF T. DEFORMANS

With a view toward making a more detailed study of the cultural variation of *T. deformans*, single spore cultures were obtained in 1941 from discharged groups of ascospores in the manner previously outlined. From a total of 215 ascospores discharged, 179, or approximately 83%, were recovered, each being used as the starting point of a monosporous culture. Each culture was designated by three symbols: a Roman numeral indicating the location of the host plant, a letter indicating the individual ascus, and an Arabic numeral indicating an individual ascospore discharged from that ascus. As an example, X–A–8 represented a culture derived from one of eight ascospores which had been discharged from a single ascus produced on an infected leaf of a peach tree growing on the Berkeley campus. Thirty-three discharging asci were used in these isolations, and of that number twenty-five discharged a complete set of eight spores, the other eight asci discharging six or seven spores. Eight complete sets of monosporous cultures out of the twenty-five were actually established in culture, while of the remaining seventeen, two to seven ascospores from each ascus were recovered.

The 179 established cultures, kept at room temperature on potato dextrose agar slants, were observed closely after several months' time in order to determine the extent of variation among the monosporous isolates from individual asci. With reference to the findings of Wieben (1927) on the segregation of sexually differentiated ascospores in the asci of the heterothallic *T. epiphylla* and *T. klebahni*, both Mix (1935) and Fitzpatrick (1934) have shown that in *T. deformans* the eight ascospores from one ascus are sexually undifferentiated, although instances of "occasional" and "incomplete" copulation between cells from different monosporous cultures were observed by Mix. This suggests that the fungus may possibly be heterothallic, and it is conceivable, therefore, that segregation of other factors could occur in the division of the diploid nucleus which might be evident macroscopically as a definite ratio of cultural types among the eight monosporous cultures derived from one ascus. No such ratio of variants appeared, however, in any of the series of monosporous cultures investigated, nor was there any evidence for the occurrence of definite ratios of morphological or physiological variants. The fact appears to be well established, therefore, that neither segregation of sex nor of other factors occurs at the initiation of the haploid phase in the life cycle of *T. deformans*.

It is not to be inferred that variation was absent in the 179 monosporous cultures, for it did occur, and quite abundantly, but not in any definite ratio among the eight cultures derived from one ascus. The cultural variation observed was in the form of variously pigmented sectors arising

sporadically, and often more than one type of sector would appear in the same colony (Plate I, Figs. 3, 4).

These cultures were maintained as stock cultures on potato dextrose agar for a period of two years, during which time they were transferred every

TABLE I

CULTURE	DATE OBSERVED	NORMAL COLOR	SECTORS		
		a	b	c	d
XII–P4	1942	x	x		
	1943	x	x		
XIII–P2	1942	x	x		
	1943	x			
XIII–O2	1942	x		x	
	1943	x			
XIII–H1	1942	x	x		
	1943	x	x		x
XIII–S4	1942	x	x		
	1943	x	x		
XIII–I1	1942	x	x	x	
	1943	x	x		
XIII–T1	1942	x	x		x
	1943	x			
XIII–P8	1942	x			x
	1943	x			
XIII–Q1	1942	x	x		
	1943	x	x		
XIII–K3	1942	x	x	x	
	1943	x			
XIII–K1	1942	x	x		
	1943	x	x		x
XIII–G4	1942	x	x		
	1943	x			x
XIII–E3	1942	x	x		x
	1943	x	x		
VI–B1	1942	x	x		
	1943	x			x

Variations in pigmentation apparent in single spore cultures of *T. deformans* in 1942 and in their sub-cultures in 1943. (*a*, pale grayish vinaceous; *b*, modifications in intensity of *a*; *c*, white; *d*, mustard or Naples yellow.)

three or four months by mass inoculations from the colony, irrespective of the sectoring. In 1942 recorded observations on the sectoring apparent in each culture were made. This was repeated in 1943 on sub-cultures of approximately the same age, and Table 1 is a tabulation of fourteen representative cultures with comparative observations for the two years. It will be noted that in three cases, the 1943 culture had the same macroscopic appearance as did the 1942 ancestral colony, while in eleven cases, the

1943 culture showed more, or less, or a different type of, variation than did the ancestral colony. Because of the technique of transfer, these results are of no significance in regard to the constancy of the variant types, but they are regarded as evidence of the abundant production of varied types of sectors in *T. deformans* maintained in culture.

ANALYSIS OF SINGLE CELL CULTURES OF T. PULCHERRIMA

Studies on the transmission [3] of the cultural variations observed in this organism were undertaken by means of the single cell technique already described. The original stock culture, which had been maintained on vegetable agar at ca. 13° C. for several years, exhibited striking dissociation into red and white areas after several weeks at room temperature on potato dextrose agar. From both the pigmented and the non-pigmented areas of this colony, mass transfers were made. The resulting colony from the white sector developed no pigment, while that from the pigmented area again produced a red colony with white sectors (Plate I, Figs. 5, 6). In all subsequent work on variation, which involved nearly 350 individual isolations during a period of 18 months, single cell technique was employed, and the cultures were maintained on potato dextrose agar at room temperature. The extent of this phase of the investigation makes it impossible to indicate clearly all results on one chart, but Figure 1 represents diagrammatically certain portions of the work. In these charts, each numeral represents an individual colony, and each group of numerals enclosed in a bracket indicates all or part of a series of single cell colonies derived from that portion of the parent colony at which the arrow originates. The actual appearance of each colony is indicated by the letters W or R, the former signifying a pure white or non-pigmented colony, and the latter signifying a red or pigmented colony. When W and R are placed together under one numeral, the colony so indicated was pigmented with one or more white sectors.

Figures 1A and 1B are examples of the most characteristic and frequent type of transmission of cultural variants found in *T. pulcherrima*. It will be noted that in Figure 1A, single cells derived from an entirely white colony give rise to pure white colonies. It will be noted in Figure 1B that cells derived from white sectors also give rise to entirely white colonies; in addition, Figure 1B shows that cells taken from the pigmented portions of colonies with white sectors will give rise to pigmented sub-colonies which again produce white sectors. It should be emphasized that these colonial phenomena — the stability of the white variants and the instability of the pigmented areas — were found constantly, without deviation, in 302 distinct single cell isolations, or in nearly 90% of the total number isolated. (Plate I, Figs. 7, 8.) Consequently, the formation of pure

[3] "Transmission" is used here and elsewhere in this paper in the sense of the reappearance of a cultural type in single cell sub-cultures. It is used in order to obviate any confusion which might arise over the use of the word "inheritance" with its connotation of sexuality.

white colonies or of red colonies with white sectors usually could be predicted merely upon the basis of the portion of the parent colony from which the single cell originated. The abundant production of totally white colonies developing on the same medium which supported the growth of pigmented

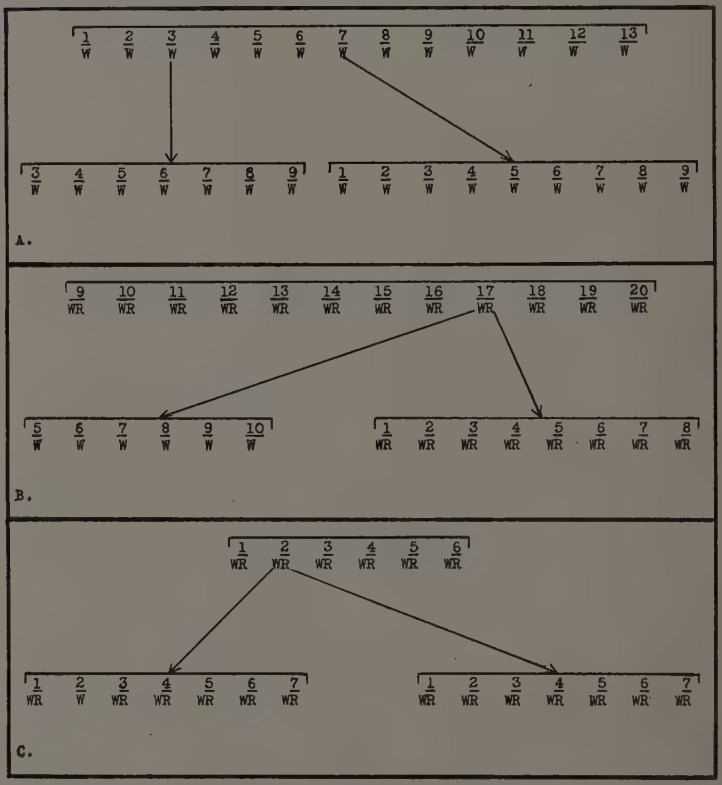
1 2 3 4 5 6 7 8 9 10 11 12 13
W W W W W W W W W W W W W
3 4 5 6 7 8 9
W W W W W W W
1 2 3 4 5 6 7 8 9
W W W W W W W W W
A.
9 10 11 12 13 14 15 16 17 18 19 20
WR WR WR WR WR WR WR WR WR WR WR WR
5 6 7 8 9 10
W W W W W W
1 2 3 4 5 6 7 8
WR WR WR WR WR WR WR WR
B.
1 2 3 4 5 6
WR WR WR WR WR WR
1 2 3 4 5 6 7
WR W WR WR WR WR WR
1 2 3 4 5 6 7
WR WR WR WR WR WR WR
C.

Fig. 1. Occurrence and transmission of cultural variants in single cell colonies of *Torulopsis pulcherrima*. (Explanation in text.)

colonies indicates that the chemical composition of this substratum appeared to play no rôle in pigment production (Porchet 1938), although Beijerinck (1918) and Castelli (1940) have advanced the idea that the formation of pigment in *T. pulcherrima* is dependent upon traces of iron salts in the medium.

However, three distinct exceptions to this phenomenon of variation were found to occur in about ten percent of the cases. In the first type, twenty-

four single cells, each derived from the marginal area of pigmented portions of parent colonies, gave rise to wholly pigmented sub-colonies which failed to develop any visible white sectors. One of these pure red colonies was subcultured, the five derived single cell colonies also being pigmented and failing to show any variation. Further subculturing from one of these resulted in five more completely red colonies. Thus, the red cultural type was not found to be completely unstable, although the possibility exists that these apparently constant red types may have produced white sectors in portions of the colony other than the surface layers and consequently were not apparent to the eye.

The second exception to the normal type of variation was the production of two small brownish sectors in the red portion of a sectored colony derived from a single cell. Single cells isolated from these brown sectors gave rise to colonies of the normal red color. It is concluded that the brownish sectors were merely temporary variants, the formation of which, therefore, presumably did not involve a mutational change (Snyder and Hansen 1939).

The final type of irregularity in cultural behaviour involved the appearance of a red pigment in single cell colonies which were derived either from the white sectors of pigmented colonies (Figure 1C) or from pure white colonies. It should be noted, however, that a preliminary examination indicated that this pigment was perhaps not identical with the normal type in that its color was usually a deeper red and it appeared to lack diffusibility. This type of variation, although of comparatively rare occurrence, is nevertheless of utmost significance in regard to the interpretation of the results of this study of cultural variation in *T. pulcherrima* as will be noted in the following discussion.

In attempting to explain the occurrence and transmission of cultural variation observed in single cell colonies of *T. pulcherrima*, emphasis should be placed upon the distinctive nature of the dissociation, in that white to white and red to red and white appeared to be the normal behaviour. This is in confirmation of the work of Punkari and Henrici (1933, 1935) who state, ". . . red is much less stable than white. It has been possible to maintain pure reds through three generations in 2 lines by selective subculturing. But white sectors appear so frequently in red colonies that we believe it will be impossible, under the conditions of this experiment to maintain a pure red line indefinitely." The lack of sporulation in their cultures was justifiably regarded by Punkari and Henrici as proof of absence of sexual reproduction, and they therefore concluded that the observed dissociation bore no relation to hybridization or to any other phase in a life cycle involving sexuality.

A possible explanation for the observed variation may lie in the investigations of Hansen (1938) on the dual phenomenon, in which a dual fungus is regarded as one which is composed of two distinct cultural homotypes, M (mycelial) and C (conidial), which may not be recognized until their separation from the heterotype MC is accomplished by single spore or single cell technique. Hansen stated that "the dual phenomenon is due to hetero-

caryosis, i.e., that individual cells and individual spores of dual fungi contain two genetically distinct types of nuclei," and he further stated in 1942 that "two factors or mechanisms operate against the possibility of the uninucleate condition being continuous or permanent," the two factors being mitosis and anastomosis. Heterocaryosis is believed to be initiated by "(1) mutation within a plurinucleate entity, and (2) by fusion or anastomoses between cells having genetically unlike nuclei." Hansen and Snyder (1943) in discussing the relationship between the dual phenomenon and sex in a species of *Hypomyces* found that in many cultures an M homotype of extreme stability arose *de novo* in C homotypes with great frequency and regularity and that the M type never reverted to the C type. They concluded, as a result of crossing behaviour, that "the change of C to M is a true genetic mutation, that it is a unidirectional one, apparently common to fungi in general. . . . ," and "that this mutation may be the cause of the dual phenomenon in all fungi where this condition occurs." Although the regular appearance of white sectors in red colonies of *T. pulcherrima* is certainly indicative of a unidirectional mutation, the actual proof of this assumption would necessarily lie in crossing experiments involving the inheritance of the factor for white sectors. Although this has not been demonstrated in this organism, it is nevertheless obvious that the stable white variant obtained in culture may be considered analogous to the mutating C homotype of these authors. In view of the uncertainty in regard to the nuclear condition in this species, the designation of the original mass isolate in regard to M and C would be a matter for speculation.

However, the exception to the normal dissociation involving the production of red from white does not support the interpretation of the variation in this organism as being an expression of the dual phenomenon because of its reversibility. Rather, it is indicative of Punkari and Henrici's "reversion to ancestral forms" (1933), in which they found that a pure white colony derived from a white sector gave rise to a mixed red and white subcolony. However, if this pigment arising in white colonies is found to be of a different nature than the normal type, the concept of reversion would not apply, and the normal dissociation could then be regarded with a degree of certainty as an expression of the dual phenomenon. Studies on this phase of the problem are now in progress.

One further point in regard to the production of pigment, regardless of its nature, in colonies derived from white sectors is of significance. Actual dissection of a three-month-old sectored colony revealed that the sector did not extend throughout the entire depth of the colony. The relatively small size of the colony and its sector made this relation rather difficult to determine, but further evidence of its existence was obtained by making mass transfers of cells from different portions of the dissected colony. It was found that transfers of cells from the base of the colony directly underneath the white sector gave rise to subsequent pigmented colonies, indicating that the white sector did not actually extend to the bottom of the colony. It is conceivable that if a transfer needle were plunged rather deeply into a sector

of this type, the cells transferred could be a mixture of both the non-pigmented and the pigmented types, and that single cell isolations could therefore give rise to both types. Further dissection of other sectored colonies of both *T. pulcherrima* and *T. deformans* revealed that the depth of the sectors may range from superficial layers of cells to an entire wedge of the colony, emphasizing the fact that accurate interpretation of results may be dependent upon the actual depth to which the transfer needle is inserted into the sectored portions of the colony. In this connection, Christensen (1940) has stated, "Sectors are not necessarily pure for type because mutants may grow either over or under the parent, and subcultures from such sectors may consist of the mutant plus the parent line." Whether or not these facts may be correlated with the apparent reversion noted from white to red is unknown, since the dissections were made on sectored colonies from other series; these facts are offered, however, as a possible explanation, although, of course, they would not apply to the production of pigment in colonies derived from pure white cultures.

Thus, it appears that because of the possibility of the occurrence of reversibility, the dual phenomenon may not be the correct explanation for the cultural variation occurring in *T. pulcherrima*. Regardless of interpretation, however, the observed facts still point to this variation as being of a distinctive type in that it has been found to be predominantly unidirectional, stable, and predictable, and, as will be discussed later, is associated with significant differences in cellular morphology.

ANALYSIS OF SINGLE CELL CULTURES OF T. DEFORMANS

The previously noted variants occurring in the form of colonial sectors in monosporous cultures of *T. deformans* were subjected to a single cell analysis similar to that made for *T. pulcherrima* in order to obtain additional information in regard to their transmission and stability. Because of the number of monosporous isolates on hand, a series of single cell isolations, each involving one or more generations, was made from each of six monosporous sectored cultures; whereas in the analysis of the cultural variants of *T. pulcherrima*, a single sectored colony had been used as the basis for all subsequent single cell work.

The single cell colonies obtained in this manner exhibited, as a group, the same range of variation in pigmentation which had been observed in their ancestral monosporous cultures, as well as a sporadic tendency to produce roughened surface areas which appeared to bear no relation to the pigmentation, and which were characterized by numerous small papillae.

Transmission of two (white and yellow) out of the three variants observed was noted, while the third type, which was characterized by various modifications in intensity of the normal pink colony color, did not appear to be transmissible. It should be noted, however, that this third type was often evident only as a slight deviation from the normal color, pale grayish vinaceous. Consequently, although quite evident in its original appearance as a colonial sector, its later recognition in sub-cultures involved some

difficulty. In spite of this, it should be emphasized that no positive evidence was obtained for the transmission of this sector type (designated as *b*), because all single cells derived from *b* sectors gave rise to colonies the color of which appeared to be essentially similar to the normal type (*a*). It is

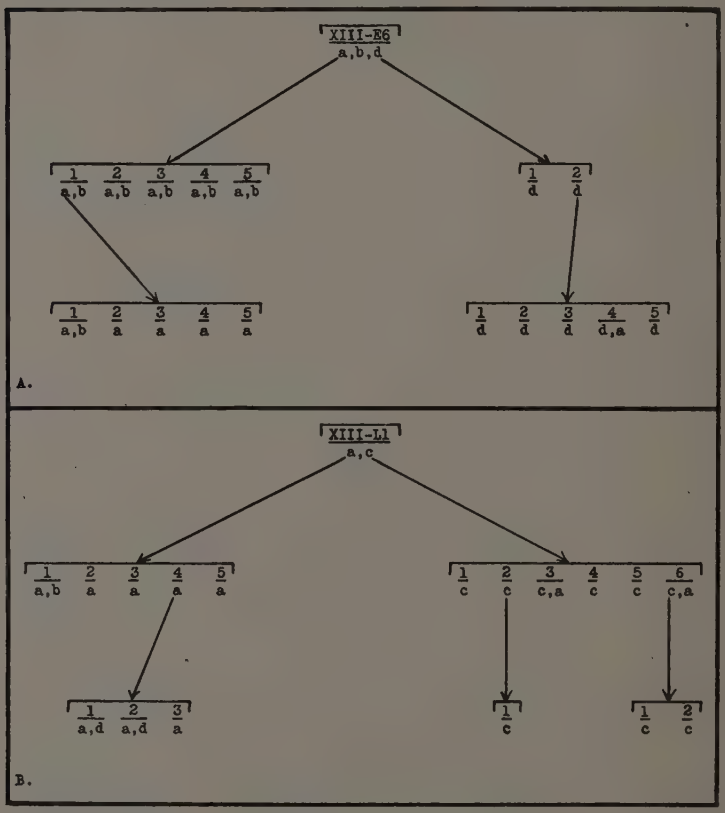

Fig. 2. Occurrence and transmission of cultural variants in single cell colonies of *Taphrina deformans*. (Explanation in text.)

therefore concluded that sectors of the *b* type were temporary variants which consequently were not produced by mutational changes.

Transmission of the other two variants is shown in Figure 2 which diagrammatically represents the single cell analysis made of two monosporous sectored colonies, XIII–E6 and XIII–L1. In these diagrams, as in those for *T. pulcherrima*, each numeral represents an individual colony,

and each group of numerals enclosed in a bracket represents a series of single cell colonies derived from that portion of the parent colony at which the arrow originates. The actual appearance of the colonies is indicated by the following symbols: *a*, the normal color, pale grayish vinaceous; *b*, modifications of *a* either by greater or lesser intensity of color; *c*, non-pigmented or white; and *d*, mustard or Naples yellow. When these letters are combined under one numeral, that colony consisted of the color indicated by the first letter, with sectors of the variant type(s) so designated.

Figure 2A exhibits three points worthy of note: (1) the transmission of the yellow variant *d*; (2) the incomplete stability of *d*, as seen by its dissociation in one colony to an *a* variant; and (3) the sporadic production of *b* variants in the normal *a* type.

Figure 2B exhibits similar phenomena: (1) the transmission of the white variant *c*; (2) the incomplete stability of *c*, as seen by its dissociation into *a* variants; and (3) the sporadic production of variants *b* and *d* in the normal *a* type.

These observations point to the main distinction apparent between the cultural variation of *T. deformans* and *T. pulcherrima* — namely, the regularity with which the latter produces a single variant as contrasted with the sporadic production of two variants by the former organism. In addition, the apparent reversion of the white variant to the parent type as observed in *T. pulcherrima* was of comparatively rare occurrence when contrasted with the abundant reversions to the normal type occurring in the variants of *T. deformans*. The two organisms are similar with respect to the production of temporary variations in the form of non-transmissible sector types — namely, the *b* variant of *T. deformans* and the brown variant of *T. pulcherrima*.

It is therefore concluded that, while the observed cultural variation in *T. pulcherrima* may possibly be regarded as an expression of the dual phenomenon, no such interpretation can be inferred from the evidence obtained from *T. deformans*. As has been previously noted, the regular occurrence of the white variant in the red cultural type of *T. pulcherrima* is indicative of a true mutation, but actual proof from inheritance studies is lacking. Likewise, crossing experiments are not possible with the homothallic *T. deformans*, so that the inheritance behaviour of the variants are unknown. In addition, the single cell analyses performed with *T. deformans* were not so extensive or of such long duration as to preclude the possibility that the yellow and the white transmissible variants may also be only temporary. As Snyder and Hansen (1939) have pointed out, "They (temporary variations) may result from some factor in the environment . . . and eventually revert to the parent type with the return of original conditions. Reversion, however, may be slow and the variants give a semblance of permanency." However, if they are to be regarded as true mutants, and the fact that they arose from monosporous cultures derived from haploid uninucleate cells is good evidence that they may well be (Christensen 1940), it should be emphasized that their spontaneous and unpredictable occur-

rence would seem to preclude the possibility of their being an expression of the dual phenomenon.

MICROSCOPIC EXAMINATION OF CULTURES

The general morphology of the cells of both organisms in culture was found to be essentially similar to the descriptions given by previous investigators, such as those of Mix (1935) on *T. deformans* and those of Lodder (1934) on *T. pulcherrima.*

Young cultures of both fungi maintained on potato dextrose agar at room temperature were composed of round to oval, thin-walled cells which reproduced vegetatively by typical budding. Both organisms produced cells of similar shape, although those of *T. pulcherrima* showed a tendency to become more globose than did those of *T. deformans.* The range in cell size was found to be similar to that previously reported for *T. deformans* (2.4–6.3 x 3.6–8.6 μ, Mix 1935) and for *T. pulcherrima* (3.0–4.5 x 3.5–6.5 μ, Lodder 1934), although somewhat larger cells were occasionally found in young cultures of the latter. The main distinction in cellular morphology between young cultures of the two organisms appeared to be in the production of oil (or fat) globules in the round cells of *Torulopsis* and their absence in the cells of *Taphrina.* These oil globules, although showing quite a range in size, were characteristically quite large, often occupying almost the entire cell. Such round cells containing a single large oil droplet have been designated by Lodder as typical "pulcherrima cells," and, according to her, were noted in the original description of the species by Lindner (1887). Numerous other investigators (Beijerinck, 1918; Grosbusch, 1915; Punkari and Henrici, 1933) of this organism have also noted them. In the present study, their occurrence was noted in young cultures, but they were found to be much more abundant in older cultures, as will be discussed below.

Old cultures (one to three months) of both fungi were, in general, quite similar microscopically and showed few significantly distinguishing characters. In addition to the normal type of vegetative cells (Plate I, Fig. 9), the abundant production of large, thick-walled, globose cells was noted in both, those of *T. pulcherrima* appearing as typical "pulcherrima cells," while those of *T. deformans*, although of similar shape, were often larger and typically contained more than one oil globule (Plate I, Figs. 10, 11). The size of these cells varied considerably in both organisms, but all were larger than the vegetative budding cells, and some reached a diameter of 12 to 15 μ. As previously mentioned, the occurrence of these large thick-walled cells in *T. pulcherrima* has been noted by many investigators, while Pierce (1900), Fitzpatrick (1934), Mix (1924, 1935), and Martin (1925, 1940) have observed them in *T. deformans.* Their significance will be discussed later.

SPORULATION

Previous reference has been made to the work of Windisch (1938, 1940), in which sporulation was reported for the first time in *T. pulcherrima.* The

results of the following microscopic investigation of this organism are offered in partial confirmation of Windisch's observations.

As previously noted, large thick-walled cells containing a single oil globule were observed to be extremely abundant in old cultures of *T. pulcherrima* on both potato dextrose and vegetable agar. In addition, it was found that many of these cells possessed what appeared to be the attached remnant of a cell wall. In view of Windisch's interpretation of similar structures representing stages in the life cycle of this organism, it was decided to investigate the species more fully for the occurrence of sporulation in culture.

It will be recalled that Windisch had observed in "pulcherrima cells" the formation of bud-like protrusions into which passed a portion of the divided oil globule and in which four spores were subsequently formed. The rupture of the protruded daughter cell liberated the spores, the remnant of this cell remaining attached to the mother cell, often for long periods of time. Copulation between cells derived from the budding of the ascospores occurred and resulted in the eventual formation of the large, thick-walled "pulcherrima cells."

Although not all stages in this life cycle were found, the following structures, believed to represent the sporulation process, were noted in both mass and single cell cultures (Plate I, Figs. 12–14; Plate II, Figs. 1–5):

Thick-walled "pulcherrima cells" with

1) papillate protrusions
2) attached daughter cells, some of which contained oil globules
3) attached daughter cells which contained one to three spore-like bodies
4) attached remnants of ruptured daughter cells

Although not clearly evident in the photomicrographs, the small bodies occurring in the attached daughter cells were readily distinguished from oil globules by the fact that they were less refractive. In addition, a small dark area, interpreted as a small oil droplet, is apparent in these bodies. It is concluded that these structures are actually spores, and that all of the structures listed above represent phases of the sporulation process. In this connection, it should be noted that the morphology of these structures was essentially similar to that described and illustrated by Windisch.

Windisch's observations on the budding of the ascogenous cells were also confirmed. He states, "Die Mutterzelle sprosst wieder aus; noch während der erste Ascus aufsitzt, kann sie durch Sprossung eine oder mehrere Tochterzellen hervorbringen, von denen sich nicht sicher entscheiden lässt, ob sie nun auch Asci werden oder Sprosszellen bleiben sollen." Such a phenomenon is illustrated in Plate II, Fig. 6, which represents the development in twenty-four hours of a "pulcherrima (ascogenous) cell" with attached, empty daughter cell (ascus), both of which had been separated together from the margin of a colony by the micromanipulator. It will be noted that in this particular case two cells have been formed from the ascogenous cell at the opposite side from the empty ascus. No further growth occurred.

Figure 6 of Plate II is also of significance in that it reveals a morphological distinction between normal buds and those buds which are believed to represent asci. It will be seen from this figure that the two vegetative cells are somewhat constricted at their bases, while the assumed ascus has a comparatively large, unconstricted base. This distinction between typical buds and asci was quite characteristic in the cultures examined and was used as a basis for differentiation in the absence of spore-like bodies.

Unfortunately, the isolate of *T. pulcherrima* used in these studies had been maintained as a stock culture for several years prior to the present investigation and appeared to be losing its sporulating ability. As a result, comparatively few spores were found, and it was not possible to study the actual sequence of events in the sporulation process of individual cells, as did Windisch. Also, Windisch had found quite consistently spores in groups of four, while in the present study, three spores were the most found in one cell. Spore discharge and germination were not observed.

A few indications of copulation of vegetative cells were noted. One non-pigmented colony was found to consist of cells which appeared to be copulating with the formation of conjugation tubes (Plate II, Fig. 7). In another non-pigmented colony, two cells were seen which were in such a position as to be indicative of the copulation process.

Windisch observed sporulation in *T. pulcherrima* and subsequently suggested the relationship of this organism to members of the genus *Taphrina* on the basis of the latter's sporulation as it occurs on the host plant. In view of this fact, it was decided to make an intensive study of the cellular morphology of *T. deformans* in culture in order to determine whether Windisch's views on the similarity of the two organisms could be further substantiated.

One- to three-month-old cultures of the fungus on potato dextrose and vegetable agar were examined microscopically and revealed the presence of large thick-walled cells containing one to many oil globules, with, in addition, attached structures similar, if not identical, to those noted above for *T. pulcherrima* (Plate II, Figs. 8–10; Plate I, Fig. 11).

The similarity of these structures to those observed in old cultures of *T. pulcherrima* is readily seen from the photomicrographs, and it is believed that the bodies occurring in the attached daughter cells of *Taphrina* may also be regarded as spores, and that likewise the attached structures may represent phases of the sporulation process. As in *T. pulcherrima*, it will be seen that each of the spore-like bodies contains what appears to be one or two small oil globules. The discharge of these bodies was not observed.

The occurrence of this apparent sporulation in *T. deformans* in culture has two significant aspects — first, it lends support to Mix's report of the occurrence of the diplophase of *T. deformans* in culture, and secondly, it further substantiates Windisch's conception of a relationship between *T. pulcherrima* and the Taphrinales.

In 1924 Mix observed large, thick-walled cells in old cultures and designated them as "resting spores." He noted that in germination they "may

burst, allowing the escape of a thin-walled protoplast, a behaviour similar to that of the ascogenous cells found in the leaf," and, in agreement with Pierce (1900), he suggested that "the resting spores developed in culture may indicate an approach to the ascigerous stage." In 1929, he reported in an abstract that the resting cells are believed to be ascogenous cells and that "structures believed to be imperfect asci have also been found." In 1935 further emergences from the germinating resting spores were noted and interpreted as asci, some of which were found with "2 and 3 fully formed spores." Other workers, such as Martin (1940) and Fitzpatrick (1934) have noted similar large, thick-walled cells in culture, but have not ascribed to them the character of ascogenous cells, for no structures resembling asci were found. Although Mix's assumed asci were comparable in size and shape to the normal asci occurring on the host, it is believed that the smaller attached daughter cells containing spore-like bodies noted here may also be regarded as imperfect asci with ascospores, and that consequently the large, thick-walled mother cells may be interpreted as ascogenous cells. It is interesting to note that the large thick-walled cells were found in both mass and monosporous cultures of *T. deformans*, indicating, as Martin (1940) has recently pointed out, that "their formation is evidently not dependent upon conjugation."

It will be recalled that Windisch interpreted the "pulcherrima cells" of *T. pulcherrima* as ascogenous cells and the bud-like protrusions developing into daughter cells as asci in which ascospores were formed. The similarity between these structures occurring in culture and the ascogenous cells, asci, and ascospores of species of *Taphrina* was then pointed out, and resulted in the conception of a close relationship between *T. pulcherrima* and the Taphrinales. It is believed that the results of the present study provide further supporting evidence for this view, because of the fact that quite similar types of cultural sporulation in both *T. pulcherrima* and *T. deformans* have been observed.

COMPARATIVE CELLULAR MORPHOLOGY OF THE CULTURAL TYPES OF T. PULCHERRIMA

Both Porchet (1938) and Windisch (1940), although aware of the variation in pigmentation occurring in *T. pulcherrima*, worked with mass rather than with single cell cultures and consequently failed to obtain a complete separation of the two pure cultural types. As a result, their observations on cellular morphology were undoubtedly made, in part, on mixtures of cultural types and are therefore of little significance in a study of the comparative cellular morphology of the pigmented colonies and their non-pigmented variants. On the other hand, Punkari and Henrici (1933, 1935) by means of single cell technique were able to separate the white variant from the pigmented portion, and, as a result of microscopic examination, concluded (1933) that "no morphologic differentiation could be established between red and white variants." The evidence obtained from the present investigation of this phase of the problem indicates, to the contrary, that

some differentiation on the basis of cellular morphology is apparent between the two cultural types.

Microscopic investigations were made of all of the single cell colonies used in the work on cultural variation, each colony or sector being examined after it had been growing on potato dextrose agar for one month or longer. The results of this study showed that the red pigmented cultural type produced abundant thick-walled cells, often containing oil globules (Plate II, Fig. 11), while the white variants, both in the form of sectors and entire colonies, often lacked this tendency and consisted, for the most part, of smaller, thin-walled cells reproducing vegetatively by typical budding [4] (Plate II, Fig. 12). This phenomenon was first noted in the original mass sectored culture on potato dextrose agar. The results of subsequent microscopic examinations of single cell colonies derived from this ancestral culture are tabulated as follows:

	Number of Cultures Examined	Number of Cultures Containing Large Thick-walled Cells	Number of Cultures Containing Large Thick-walled Cells with Attached Daughter Cells
Red Cultural Type	44	40	31
White Cultural Type	141	10	3
Total	185	50	34

It should be noted that some cellular structures occurring in both the red and white cultural types were rather difficult to classify because of transitional stages in size and shape, due, it is believed, to the age of the culture and the portion of the colony from which the cells to be examined were taken. Furthermore, oil globules were not always apparent in the large cells, and for this reason they have not been designated as "pulcherrima cells" in the above tabulation. It is believed, however, that the large, thick-walled cells observed, either with or without oil globules, may be regarded as similar to those cells interpreted by Windisch as ascogenous cells, for many of them were found to possess attached daughter cells. Likewise, the attached daughter cells are considered to be asci, for several of these were found to contain spore-like bodies.

Because of the occurrence of large, thick-walled cells and attached daughter cells in some of the white variants, this tabulated evidence cannot

[4] In 1918 Beijerinck, working with mass cultures, noted that certain cells of *Saccharomyces pulcherrimus* (*Torulopsis pulcherrima*) failed to produce fat globules. This was considered to involve a mutational change, and such variants were designated as *S. pulcherrimus secundarius*. Although fairly constant, these so-called mutants were found to show in some cases a tendency to revert to the normal condition and were apparently not related to any constant directional change in pigmentation. Hence it is believed that this behaviour is not comparable to that which has been found in the present study, although the possibility exists that the results would have been similar if Beijerinck had employed single cell technique.

be regarded as implying a definite, constant distinction between the two cultural types on the basis of cellular morphology. It can be regarded, however, as indicative of different morphological *tendencies* in the two types. In view of Windisch's interpretation of these cellular structures, this evidence raises interesting implications in regard to the relationship between the life cycle of this organism and its cultural variation. Certainly, a tendency for the sexual stage to occur more frequently in the red cultural type is indicated here, but the complete answer to this problem must await the results of further investigations.

Although some secondary papillae and roughened surfaces were evident in several single cell cultures of *T. pulcherrima*, no detailed study of them was undertaken. It should be mentioned, however, that one pure white single cell colony produced two large craters, and microscopic examination of cells from both of them revealed the presence of long, septate mycelial strands. This is in confirmation of Punkari and Henrici's investigations (1935), in which they noted that craters were only observed in white colonies and stated that ". . . microscopic examination of colonies with craters always showed the presence of mycelium, which was not found in smooth colonies."

In addition, twelve white colonies or sectors, when examined microscopically, were found to consist of polymorphic cells, or of cells exhibiting a pseudomycelial tendency, and it was further noted that these were always associated with a roughened surface characterized by the formation of numerous small papillae.

COMPARATIVE CELLULAR MORPHOLOGY OF THE CULTURAL TYPES OF T. DEFORMANS

Similar microscopic investigations were carried out on all of the single cell colonies of *T. deformans* in order to determine whether any variation in cellular morphology existed, and if so, whether it bore any relation to the formation of the four cultural types previously designated on the basis of pigmentation as *a*, *b*, *c*, and *d*. All colonies were examined after they had been growing on potato dextrose agar slants for one month or more, and recorded descriptions were made of the general appearance of the cells, including the occurrence of large, thick-walled cells either with or without attached daughter cells. In view of the fact that spore-like bodies were found in several of these attached daughter cells, these cellular structures were regarded as being indicative of the sporulation process and were consequently interpreted as ascogenous cells, attached asci, and spores. As in the microscopic investigations of *T. pulcherrima*, some difficulty was encountered in accurately interpreting all structures observed because of the occurrence in some colonies of cells of transitional shape and size.

In general, it can be stated that these cellular structures indicative of sporulation occurred as abundantly as in *T. pulcherrima*, being found in 62 out of a total of 159 cultures examined. (Compare with tabulation totals for *T. pulcherrima*, page 366.) In contrast to the observations on *Torulopsis*,

however, no evidence was obtained in this study for a differentiation of the cultural types on the basis of cellular morphology, for these structures were found in representatives of all four cultural types. They appeared to be somewhat more abundant in the normal *a* type, but it is believed that they were found in sufficient numbers in the variants *b*, *c*, and *d* to preclude any generalization as to a constant relationship between sporulation and pigmentation.

These results seem to indicate, therefore, that in *T. deformans* cellular morphology, with regard to the occurrence of structures indicative of sporulation, appears to be more constant than in *T. pulcherrima*, in the sense that it shows no clear-cut differentiation into two types, each associated with a distinct pigmented cultural type. On the contrary, in *Taphrina*, the occurrence of cells indicative of sporulation may appear in any culture regardless of its pigmentation. It is possible that their occurrence may be correlated with the age of the culture, but this is offered only as a theoretical consideration, for no detailed study was made of this phase of the problem.

A tendency for mycelial production in culture, which is believed to be more pronounced than has previously been reported, was also noted in *T. deformans*. Long, septate hyphal strands very similar in appearance to the intercellular mycelium of this organism in host tissue were observed (Plate III, Figs. 1, 2). This tendency was noted in the normal type, as well as in the *b* variant and was not found to be associated in every instance with a roughened surface.

Other cultures of *T. deformans* were composed of elongated, rod-shaped, or otherwise irregularly shaped cells which were either single or in pairs. In addition, the formation of primitive pseudomycelium in the form of short chains was noted by both the normal and irregularly shaped cells. These pseudomycelial and polymorphic tendencies occurred in the normal pigmented type as well as in the *b* variant and were found either in association with roughened surfaces or independent of them. A tendency to produce elongated or rod-shaped cells was also noted in some of the smooth colonies of the yellow variant *d*.

NUCLEAR CONDITION

Considerable difficulty was encountered in obtaining a satisfactory nuclear stain for *T. pulcherrima*. The most successful stain employed was Laustsen's modification of the Feulgen technique, as described by Winge (1935). Windisch had apparently obtained very satisfactory results with this method, although no photomicrographs of stained preparations were included in his paper. He states (1940): "Kernfarbungen nach Winge-Feulgen mit Fuchsin erwiesen die Zweikernigkeit aller vegetativen Formen sowie der Ascusmutterzellen."

In the present study, cells from young, active cultures were the only ones stained satisfactorily by this method, and consequently no information as

to the nuclear condition of the large, thick-walled cells (ascogenous cells or ascus mother cells) occurring in old cultures was obtained. However, it was found that all vegetative cells, whether from mass or single cell, pigmented or non-pigmented cultures, were stained in such a way that they exhibited what is believed to represent a constant uninucleate condition. This is in direct contrast to the binucleate condition reported by Windisch.

Although some differences in interpretation of the stained bodies could be made, it will be seen from Plate III, Figs. 3, 4 that these stained preparations cannot possibly be regarded as being indicative of a binucleate condition, for each cell contains a single, deeply stained body. The difficulty in interpretation appears to involve the nucleoli and the nuclear membranes. A comparison of Plate III, Figs. 3, 4 with Figs. 11, 12, 13, 14, and 15 of Plate II in Winge's paper (1935) shows a definite similarity in the results of employing this staining procedure, notwithstanding the fact that two different yeasts were involved. Winge interprets, without question, the deeply stained bodies as nuclei, but it is possible that the stained bodies in our preparations may be nucleoli, because of the fact that some of them appear to be surrounded by a definite, clear area which is not apparent in Winge's photomicrographs. This clear area may possibly represent the extent of a single nucleus and the enclosed stained body, the nucleolus, but because no membrane is visible at the periphery of the clear area, this interpretation is doubtful. Regardless of the interpretation of the nuclear details, the results of this staining method clearly indicate that the young vegetative cells of *T. pulcherrima* are uninucleate.

In contrast, all of Windisch's stained preparations revealed a binucleate condition of the cells. Consequently, he believed that the uninucleate, haploid phase of the life cycle must be of very short duration, the derivatives of the ascospores copulating very soon after spore discharge, resulting in the establishment of the binucleate stage. Windisch actually observed this fusion of ascospore derivatives (which appeared to involve dissimilar partners and therefore can be considered as heterogamous copulation), but it should be emphasized that although this plasmogamy was found to result in the dicaryon phase, the actual point in the life cycle at which karyogamy occurred was not ascertained. Windisch had consistently observed a binucleate condition in the ascogenous cells and believed that these two nuclei corresponded to the nuclear pair observed in the vegetative cells. The possibility that the two nuclei were diploid daughter nuclei of a zygote nucleus was offered, but because, under certain conditions, the ascogenous cells could reproduce vegetatively by budding instead of forming asci, led Windisch to prefer the assumption that the two nuclei in the ascogenous cell were haploid. Because uninucleate ascogenous cells were never observed, Windisch proposed the idea that karyogamy in *T. pulcherrima* may occur in the ascus, and as evidence of a similar occurrence in the Taphrinales, he referred to the statement of Kniep (1928) that in *Taphrina*

nuclear fusion occurs in the ascus. However, it has recently been definitely established by Martin (1940) that karyogamy in *T. deformans* occurs only in the ascogenous cells, a fact which has been generally regarded as typifying the genus as a whole (Eftimiu 1927, Gäumann and Dodge 1928).

It is therefore believed that Windisch's assumption of a similarity between *T. pulcherrima* and *Taphrina* spp. based upon the nuclear condition in the life cycles of these organisms is incorrect. The possibility exists, of course, that karyogamy does occur in the ascogenous cells of *T. pulcherrima* and that Windisch had failed to observe it; but until this fact is actually known, a concept of a relationship between *Torulopsis* and *Taphrina* on the basis of the nuclear behaviour known at present does not appear to be justified.

The Laustsen modification of the Feulgen technique was not found to be satisfactory for demonstrating the nuclei in cells of *T. deformans*. None of the stains employed was found to be completely successful, although the use of Mayer's haem-alum demonstrated the presence of a single stained body in some of the sprout conidia from young cultures. Although no detail was apparent in any of these bodies, they were regarded as being indicative of a uninucleate condition, in view of the fact that several investigators (Fitzpatrick 1934, Martin 1940, Mix 1935) have found this to be the case in the majority of cells from young cultures of *T. deformans*.

Because, as in *Torulopsis*, only active cells from young cultures were successfully stained, no information on the nuclear condition of the larger, thick-walled cells (ascogenous cells) was obtained, although Mix reported them as being either uni- or binucleate (1935). In addition, Fitzpatrick (1935) observed some binucleate sprout conidia taken from fairly old cultures, while Wieben (1927) found in *Taphrina* spp. binucleate conidia following copulation. In the present study, no binucleate cells were observed.

PHYSIOLOGICAL TESTS

Although comparative observations of the microscopic and macroscopic appearances of the two fungi in culture represented the main problem in the present investigation, a limited number of tests were performed in order to determine some of the physiological differences between the two organisms as well as between the variant cultural types of each organism.

One of the most important distinctions between the physiology of *T. deformans* and *T. pulcherrima* is that the former has been reported to lack the ability to produce alcoholic fermentation (Mix 1924), while *T. pulcherrima* is a species capable of fermenting glucose, fructose, and mannose (Lodder 1934). Mix in 1924 used 10% solutions of dextrose, sucrose, and maltose in potato broth in his fermentation tests and had obtained completely negative results. Confirmation of this work was obtained by the failure of active mass and single cell cultures of *T. deformans* to produce any fermentation of 2% solutions in yeast juice of galactose, glucose,

maltose, lactose, and sucrose. In addition, the three variant types, *b*, *c*, and *d* were found unable to cause fermentation of any of these sugars.[5]

Because of this lack of fermentative ability in *Taphrina*, tests were performed by means of the auxanogram method (Lodder 1934) in order to determine what sugars this organism was capable of assimilating under aerobic conditions. Positive results were obtained with glucose and sucrose, and negative results with galactose, lactose, and maltose.

T. pulcherrima, on the other hand, was found to be capable of fermenting a 2% solution of glucose. In addition, the appearance in some of the sucrose solutions of a few gas bubbles was noted, which may be regarded as being indicative of a slight tendency of this organism to ferment this sugar. However, the explanation for the occurrence of gas bubbles in the sucrose solutions may lie in the method of sterilization of the liquid media. As Mudge (1917) pointed out, disaccharides may become hydrolyzed by sterilization in both the autoclave and the Arnold sterilizer, resulting in the formation of monosaccharides in the medium. Mudge found this to be the case with maltose and lactose, and the possibility exists that the sucrose solutions used in the present tests were sterilized for a length of time sufficient to induce a partial breakdown into the monosaccharides glucose and fructose, both of which are fermented by this organism. It should be noted, however, that, although Lodder in her standard work on generic and specific determination of the imperfect yeasts lists glucose (fructose, mannose) as the only sugar fermented by *T. pulcherrima*, Grosbüsch (1915) found that a strain of *Torula rubefaciens* (*Torulopsis pulcherrima*) was able to cause a very slight fermentation of sucrose.

Galactose, lactose, and maltose gave negative results in all fermentation tests with *T. pulcherrima*. In addition, no differences in fermentative ability were found between the red and the white cultural types.

Nitrogen utilization tests were undertaken by means of the auxanogram technique. Both the red and the white cultural types of *T. pulcherrima* were found capable of utilizing only asparagine and peptone, although Lodder had obtained, in addition, positive results with ammonium sulfate and urea. In this connection, it is worthy of note that in the original unpublished identification of this isolate of *T. pulcherrima*, ammonium sulfate was found by E. M. Mrak to be slowly utilized, while urea was not utilized at all.

No positive results for the utilization of any nitrogen-containing substances by *T. deformans* were obtained by means of the auxanogram method. In view of the fact that peptone is generally utilized as a nitrogen source by yeasts, as well as ammonium sulfate (Henrici 1941), these results are surprising. Moreover, in the sugar auxanograms, ammonium sulfate was the only nitrogen source available in the basal medium and therefore must have been utilized by *T. deformans* as evidenced by its growth in the

[5] According to the well-known "Kluyver-Dekker laws" (as cited by Henrici 1941), any yeast which can ferment glucose can also ferment fructose and mannose. For this reason, fructose and mannose were not included in the fermentation tests.

presence of glucose and sucrose. It is concluded that the complete explanation of these negative results must therefore await the results of further investigation.

In general, the physiological tests, although limited in scope, appear to point to two facts worthy of consideration: 1) *T. pulcherrima* can be distinguished from *T. deformans* on the basis of its ability to ferment certain sugars, and 2) on the basis of these tests, no differences in physiological behaviour were found between the two cultural types of *T. pulcherrima* and among the four cultural types of *T. deformans.*

DISCUSSION AND CONCLUSIONS

As evidenced by cultural similarities, the results of this investigation point to the apparent interrelationship of a saprophytic yeast, *Torulopsis pulcherrima,* and a parasitic fungus possessing a yeast-like saprophytic stage, *Taphrina deformans.*

It will be recalled that this comparative study was undertaken with the hope of obtaining additional information which could be used either in substantiation or in rejection of Windisch's concept of a relationship between *T. pulcherrima* and the genus *Taphrina* and his proposal to incorporate *T. pulcherrima* in the order Taphrinales as *Candida pulcherrima.* This proposal was based upon the similarities between the observed life cycle, including sporulation, of *T. pulcherrima* and of *C. tropicalis* in culture and the previously described life cycles of *Taphrina* spp. in their parasitic, non-culturable stages. Windisch made no recorded observations on the cultural characteristics of any species of *Taphrina.* In the present study, the genus *Candida* was not investigated, and while *T. deformans* was the only species of *Taphrina* used, it is believed to be representative of the general cultural behaviour of the genus as a whole.

For purposes of comparison, the information obtained from a study of the two fungi in culture may be tabulated as follows:

That the two fungi are, in general, quite similar in cultural behaviour is clearly evident from the above tabulation. In both organisms cultural variation may occur in the form of variously pigmented, transmissible or non-transmissible growth types; cellular morphology is of a similar type, pseudomycelium or true mycelium may be found, and cellular structures indicative of sporulation frequently occur. This latter fact is regarded as one of importance for the following reasons: 1) it confirms Windisch's report of sporulation in *T. pulcherrima* and consequently justifies the removal of this organism from the imperfect yeasts; 2) it supports Mix's observations on the occurrence of the diplophase and sexuality in *T. deformans* in culture; and 3) it offers additional support for the view of a general relationship between *T. pulcherrima* and the Taphrinales. Moreover, the finding of pseudomycelium and true mycelium in *T. pulcherrima* is indicative of the fact that it does not properly belong in the sub-family Torulopsidoideae as defined by Lodder (1934).

	T. pulcherrima	*T. deformans*
Character of cultural growth	Yeast-like	Yeast-like
Characteristic color of colony	Red — non-carotinoid, diffusible pigment	Pink — non-carotinoid, non-diffusible pigment
Occurrence of variation in pigmentation	White, brown	White, yellow, and various modifications of pink
Occurrence of transmissible variants	Predictable occurrence of white sectors	Unpredictable occurrence of yellow and white sectors
Occurrence of temporary variants	Unpredictable, rare occurrence of brown sectors	Unpredictable, frequent occurrence of sectors of various modifications of pink
General appearance of cells from young cultures	Oval-globose, thin-walled, budding cells and "pulcherrima cells"	Oval-globose, thin-walled, budding cells
General appearance of cells from old cultures	Mainly "pulcherrima cells"	Similar large, thick-walled cells but with many oil globules
Occurrence of cellular structures indicative of sporulation	Abundant in old cultures and interpreted as ascogenous cells, attached asci, and ascospores	Abundant in old cultures and interpreted as ascogenous cells, attached asci, and ascospores
Occurrence of differences in cellular morphology among the various cultural types	Evident in red and white cultural types	Not evident
Occurrence of a mycelial tendency	Present	Present
Nuclear condition of young vegetative cells	Uninucleate	Uninucleate
Fermentative ability	Ferments glucose	Incapable of fermenting glucose or any other sugar
Occurrence of physiological differences among the various cultural types	Not evident	Not evident

It will be noted from the above tabulation that the chief distinguishing points between the two organisms appear to involve the type of pigmentation and the fermentative ability, but it is known that both fungi may produce a non-pigmented growth type and that the genus *Torulopsis* contains several species which lack the ability to produce alcoholic fermentation (Lodder 1934). *T. deformans*, although customarily isolated from its host by means of discharging ascospores, also may be isolated in its overwintering, saprophytic stage from peach bark or buds; it is possible that confusion in identification would result if such isolates were studied according to the present methods for the determination of yeasts, without the use of inoculation tests.

Thus, in partial support of Windisch's views, it can be said that the

cultural similarities evident between *T. pulcherrima* and *T. deformans* are indicative of their interrelationship, an assumption which is believed to be further justified by the sporulation phenomenon, which was previously reported for *T. pulcherrima* by Windisch (1938, 1940) and which, in the present study, appears to have been confirmed for that species, and, in addition, to have been found in *T. deformans*.

However, certain other facts, as yet unexplained, have been revealed by this comparative investigation which do not lend themselves to a complete substantiation of the proposals of Windisch.

Specifically, all of the evidence obtained in this study is indicative of a constant uninucleate condition in the young vegetative cells of both *T. deformans* and *T. pulcherrima*, in contrast to Windisch's report of a constant binucleate condition in *T. pulcherrima* (exclusive of an assumed, very short, uninucleate phase). This discrepancy, coupled with Windisch's belief that karyogamy in this fungus occurs in the ascus, does not support the concept of a relationship between *Torulopsis* and *Taphrina* based upon nuclear behaviour. It is believed that perhaps the explanation for this discrepancy may lie in the use of single cell technique in the present study, and the subsequent distinctive type of variation in pigmentation which it revealed. It was found, in contrast to the investigations of Punkari and Henrici, that dissociation in *T. pulcherrima* into the two cultural types, regardless of whether it is an expression of the dual phenomenon, was apparently correlated with variation in cellular morphology, and that these distinct morphological tendencies seemed to bear some relation to the sporulation process, and therefore to sexuality. Consequently, until further cytological investigations of this organism reveal the complete facts surrounding the nuclear cycle, it seems unwise to point to the observed uninucleate condition of both *Taphrina* and *Torulopsis* in culture as being indicative of their interrelationship.

Thus, it is believed that these preliminary cultural investigations lend support to the ideas advanced by numerous investigators in regard to a general relationship between the yeasts and the Taphrinales. It is further believed that they also support the recent, more specific proposal of Windisch in regard to a relationship between the Taphrinales and *T. pulcherrima*, as well as the removal of the latter from the imperfect yeasts. However, because our knowledge of the cytology, sexuality, and variation of *T. pulcherrima* is still in an imperfect state, it is believed that further investigations of a wide number of isolates of this species are needed before it can be placed with certainty into any of the present schemes of classification of the perfect fungi.

It is therefore concluded that, although our present knowledge points to a relationship between *T. pulcherrima* and the Taphrinales, until the life cycle of the former has been completely worked out, especially with regard to the nuclear behaviour and the relationship between sexuality and cultural variation, the similarities recognized at present are not sufficient grounds for adopting Windisch's proposals of transferring *T. pulcherrima* to the

genus *Candida* and of incorporating it in the Taphrinales in a new family, the Candidaceae.

It should be added that no evidence was obtained from either organism which would fully support the findings of Todd and Herrmann in regard to their assumed life cycle of *Cryptococcus hominis* (*Torulopsis neoformans*) and that consequently the transfer of *T. pulcherrima* to the genus *Debaryomyces* has not been considered.

SUMMARY

1. Both *Torulopsis pulcherrima* and *Taphrina deformans* presented a similar yeast-like appearance when grown at room temperature on potato dextrose agar.

2. Both fungi produced a reddish or pinkish non-carotinoid pigment, that of *T. pulcherrima* being diffusible and that of *T. deformans* being non-diffusible.

3. In *T. pulcherrima* a predictable mutation-like change involving the production of white sectors occurred with great regularity in pigmented colonies. In *T. deformans* unpredictable sectoring involving a color change from pink to yellow or white occurred frequently but sporadically. The white variant of *T. pulcherrima* and the yellow and white variants of *T. deformans* were transmissible but did not possess complete stability.

4. Cellular morphology was essentially similar in cultures of both organisms, which were composed of single, ovoid to globose, budding cells. In addition, a mycelial tendency was noted in both organisms.

5. In old cultures of both fungi, cellular structures indicative of sporulation were noted and were interpreted as ascogenous cells, asci, and ascospores.

6. In *T. pulcherrima* a tendency for a differentiation of the red and the white cultural types on the basis of cellular morphology was noted and was found to be correlated with the sporulation phenomenon. In *T. deformans* no such morphological differentiation among the three cultural types was evident.

7. A constant uninucleate condition was found in the young vegetative cells of both fungi.

8. *T. pulcherrima* was found capable of fermenting glucose, while *T. deformans* was found incapable of causing fermentation. No evidence was obtained from either organism for the occurrence of any physiological differences among their various cultural types.

9. On the basis of these results, the interrelationship of *T. pulcherrima* and *T. deformans* is discussed, with especial reference to the recent proposal of Windisch in regard to the removal of *T. pulcherrima* from the imperfect yeasts to the Taphrinales.

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LITERATURE CITED

De Bary, A. Vergleichende Morphologie der Pilze, Mycetozoen, und Bacterien. Engelmann, Leipzig, 1884.

Beijerinck, M. W. Levures chromogènes. — Nouvelle réaction biologique du fer. Arch. Neerland. Physiol. Homme et Anim. **2:** 609–615. 1918.

Bessey, Ernst A. A Textbook of Mycology. Blakiston, Philadelphia, 1935.

———. Some problems in fungus phylogeny. Mycologia **34:** 355–379. 1942.

Castelli, Tommaso. Considerazioni sulla *Torulopsis pulcherrima*. Arch. Mikrobiol. **11:** 126–136. 1940.

Chamberlain, Charles J. Methods in Plant Histology. 5th rev. ed., University of Chicago, 1932.

Christensen, J. J. The origin of parasitic races of phytopathogenic fungi through mutation. *In* The Genetics of Pathogenic Organisms, Science Press (A.A.A.S.), pp. 77–82. 1940.

Eftimiu, P. Contribution à l'étude cytologique des Exoascées. Le Botaniste **18:** 1–154. 1927.

Fitzpatrick, R. E. The life history and parasitism of *Taphrina deformans*. Sci. Agr. **14:** 305–326. 1934.

Gäumann, Ernst A. & Carroll W. Dodge. Comparative Morphology of the Fungi. McGraw-Hill, N. Y., 1928.

Giordano, A. Studio micologico del *Debaryomyces neoformans* (Sanfelice) Red., Cif. et Giord. e significato delle specie nella patologia animale. Mycopathologia **1:** 274–304. 1938–39.

Grosbüsch, J. Über eine farblose, stark roten Farbstoff erzeugende *Torula*. Centbl. Bakt. II, **42:** 625–638. 1915.

Guilliermond, A. La sexualité, le cycle de développement, la phylogénie, et la classification des levures d'àpres les travaux récents. Extrait des Ann. des Fermentations **2:** 129, 257, 474, 540 (Paris, 1937).

Hansen, E. C. Grundlinien zur Systematik der Saccharomyceten. Centbl. Bakt. II, **12:** 529–538. 1904.

Hansen, H. N. The dual phenomenon. Mycologia **30:** 442–455. 1938.

———. Heterocaryosis and variability. Phytopath. **32:** 639–640. 1942.

——— **& R. E. Smith.** The mechanism of variation in imperfect fungi: *Botrytis cinerea*. Phytopath. **22:** 953–964. 1932.

——— **& W. C. Snyder.** The dual phenomenon and sex in *Hypomyces solani* f. *cucurbitae*. Amer. Jour. Bot. **30:** 419–422. 1943.

Henrici, Arthur T. The yeasts, genetics, cytology, variation, classification and identification. Bact. Rev. **5:** 97–179. 1941.

Kniep, Hans. Die Sexualität der niederen Pflanzen. Fischer, Jena, 1928.

Koch, L. W. Studies on the overwintering of certain fungi parasitic and saprophytic on fruit trees. Canad. Jour. Res. **11:** 190–206. 1934.

Lindner, P. Wochenschrift f. Brauerei, **4:** 853. 1887. (Cited from Lodder.)

Lodder, J. Die Hefesammlung des "Centraalbureau voor Schimmelcultures." Beitrage zu einer Monographie der Hefearten. II. Die anaskosporogenen Hefen. Erste Halfte. K. Akad. Wet., Verhand. (2nd Sect.) D1. **32:** 1–256. 1934.

Martin, Ella M. Cultural and morphological studies of some species of *Taphrina*. Phytopath. **15:** 67–76. 1925.

———. The morphology and cytology of *Taphrina deformans*. Amer. Jour. Bot. **27:** 743–751. 1940.

Mix, A. J. Biological and cultural studies of *Exoascus deformans*. Phytopath. **14:** 217–233. 1924.

———. Further studies on the Exoascaceae. Phytopath. **19:** 90. 1929. (Abstract).

———. The life history of *Taphrina deformans*. Phytopath. **25:** 41–66. 1935.

Mrak, E. M., H. J. Phaff, & H. C. Douglas. A sporulation stock medium for yeasts and other fungi. Science **96:** 432. 1942.

Mudge, Courtland S. The effect of sterilization upon sugars in culture media. Jour. Bact. **2:** 403–415. 1917.

Pierce, Newton B. Peach leaf curl: its nature and treatment. U.S.D.A., Div. Veg. Physiol. & Path. Bull. **20:** 204 pp. 1900.

Porchet, Berthé. Contribution à l'étude de la levure *Torulopsis pulcherrima*. Ann. des Fermentations **4**(7): 385–405. 1938.

Punkari, Laila & Arthur T. Henrici. A study of variation in a chromogenic asporogenous yeast. Jour. Bact. **26:** 125–138. 1933.

———. Further studies on spontaneous variations of *Torula pulcherrima*. Jour. Bact. **29:** 259–267. 1935.

Rawlins, Thomas E. Phytopathological and Botanical Research Methods. Wiley, N. Y., 1933.

Redaelli, P., R. Ciferri, & A. Giordano. *Debaryomyces neoformans* (Sanfelice) nobis, nov. comb., pour les espèce du groupe *Saccharomyces hominis-Cryptococcus neoformans-Torula histolytica*. Boll. Sez. Ital., Soc. Intern. Microbiol. I–II: 1–7. 1937. (Cited from Henrici). [Corrected citation, **9**(1–2): 24–28. 1937]

Reess, M. Botanische Untersuchungen uber die Alkoholgärungspilze. Leipzig, 1870.

Ridgway, Robert. Color Standards and Color Nomenclature. Author, Washington, D. C., 1912.

Snyder, William C. & H. N. Hansen. The importance of variation in the taxonomy of the fungi. 6th Pacific Sci. Congr., Proc. **4:** 749–752. 1939.

Todd, Ramona L. & Walter W. Herrmann. The life cycle of the organism causing yeast meningitis. Jour. Bact. **32:** 89–103. 1936.

Wieben, Magdalena. Die Infektion, die Myzelüberwinterung, und die Kopulation bei Exoasceen. Forsch. Geb. Pflanzenkr. u. Immunität **3:** 139–176. 1927.

Windisch, Siegfried. Zur Kenntnis der Ascosporenbildung bei *Torulopsis pulcherrima* (Lindner) Saccardo. Arch. Mikrobiol. **9:** 551–554. 1938.

———. Entwicklungsgeschichtliche Untersuchungen an *Torulopsis pulcherrima* (Lindner) Saccardo und *Candida tropicalis* (Castellani) Berkhout. Ein Beitrag zur Systematik der Gärungsmonilien. Arch. Mikrobiol. **11:** 368–390. 1940.

Winge, O. On haplophase and diplophase in some Saccharomycetes. Compt. Rend. Trav. Lab. Carlsberg, Ser. Physiol. **21:** 77–111. 1935.

EXPLANATION OF PLATE I

Fig. 1. *T. deformans.* Glass needle of micromanipulator drawing out a single cell from the margin of a colony. (135x).

Fig. 2. *T. pulcherrima.* A day-old colony originating from a single cell withdrawn from the margin of the parent colony by means of the glass needle of the micromanipulator. (135x).

Fig. 3. *T. deformans.* A 3-month-old colony on potato dextrose agar originating from a single ascospore. Note abundant sectoring. (Natural size).

Fig. 4. *T. deformans.* A 3-month-old colony on potato dextrose agar originating from a single ascospore. Note absence of sectoring. (Natural size).

Fig. 5. *T. pulcherrima.* A 3-month-old pigmented colony on potato dextrose agar originating from a mass transfer of cells from the pigmented portion of the original stock culture. Note formation of white sectors. (Natural size).

Fig. 6. *T. pulcherrima.* A 3-month-old white colony on potato dextrose agar originating from a mass transfer of cells from a white sector in the original stock culture. Note absence of pigmentation. (Natural size).

Fig. 7. *T. pulcherrima.* A month-old pigmented colony on potato dextrose agar originating from a single cell of the pigmented portion of a sectored colony. Note formation of white sectors. (Natural size).

Fig. 8. *T. pulcherrima.* A month-old white colony on potato dextrose agar originating from a single cell of a white sector. Note absence of pigmentation. (Natural size).

Fig. 9. *T. deformans.* Normal type of vegetative cells (sprout conidia) from a 2-month-old single cell culture. Unstained. (588x).

Fig. 10. *T. pulcherrima.* Typical "pulcherrima cells" from a month-old, pigmented, single cell culture. Note single oil globules, thick walls, and attached cell wall remnants. Unstained. (1200x).

Fig. 11. *T. deformans.* Large thick-walled cell from a 4-month-old mass culture. Note numerous oil globules and the attached remnant of a cell wall. Unstained. (1101x).

Fig. 12. *T. pulcherrima.* "Pulcherrima cells" from a pigmented, month-old, single cell culture, showing a papillate protrusion. Unstained. (1200x).

Fig. 13. *T. pulcherrima.* A "pulcherrima cell" from a pigmented, 4-month-old, mass culture, showing the attached daughter cell. Note that both mother and daughter cells contain a single oil globule. Unstained. (1101x).

Fig. 14. *T. pulcherrima.* A large "pulcherrima cell" (11.2 μ in diameter) from a culture grown on peach leaf agar, showing an attached, intact, empty daughter cell. Unstained. (1200x).

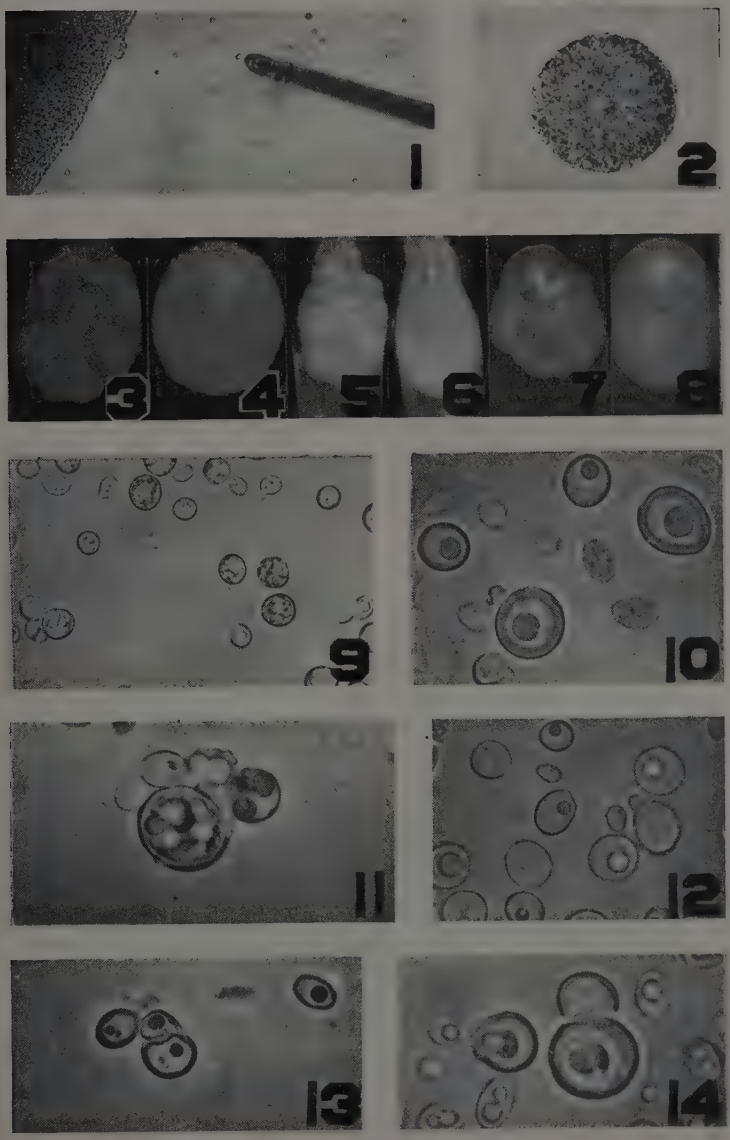


PLATE I

EXPLANATION OF PLATE II

Fig. 1. *T. pulcherrima.* A large "pulcherrima cell" from a pigmented, 2-month-old, single cell culture, showing an attached, intact, empty daughter cell. Unstained. (1200x).

Fig. 2. *T. pulcherrima.* A "pulcherrima cell" from a pigmented, 4-month-old, mass culture, showing an attached daughter cell containing one spore-like body. Note the single oil globules in the mother cell and in the spore-like body. Unstained. (1101x).

Fig. 3. *T. pulcherrima.* "Pulcherrima cells" from a pigmented, 3-month-old, mass culture, showing one cell which possesses an attached daughter cell containing two spore-like bodies. Unstained.

Fig. 4. *T. pulcherrima.* A "pulcherrima cell" with a single oil globule from a pigmented, 4-month-old, mass culture, showing the attached remnant of a daughter cell. Unstained. (1101x).

Fig. 5. *T. pulcherrima.* A "pulcherrima cell" with a single oil globule and the attached remnant of a daughter cell. From same culture noted in Fig. 4. Unstained. (1200x).

Fig. 6. *T. pulcherrima.* Growth after 24 hours from a single thick-walled cell with attached empty daughter cell, both of which had been withdrawn together from the margin of a colony. Note that only 2 cells were produced during this time. Unstained. (588x).

Fig. 7. *T. pulcherrima.* Cells from a non-pigmented, single cell colony which appear to show evidences of copulation. The long outgrowths may be regarded as conjugation tubes. Stained with cotton blue in lactophenol. (867x).

Fig. 8. *T. deformans.* Two large cells, one with many oil globules and a papillate protrusion, and the other with a single oil globule and an attached, intact, empty daughter cell. From a 4-month-old mass culture. Unstained. (1101x).

Fig. 9. *T. deformans.* Cell from a 6-month-old single spore culture, showing a thick-walled cell with an attached daughter cell containing a single oil globule (or perhaps a spore-like body). Unstained. (1101x).

Fig. 10. *T. deformans.* Large cell with attached daughter cell containing 2 spore-like bodies. Note oil globules within spore-like bodies. From same culture noted in Fig. 8. Unstained. (1101x).

Fig. 11. *T. pulcherrima.* Typical "pulcherrima cells" from a pigmented, month-old, single cell colony. Unstained. (1200x).

Fig. 12. *T. pulcherrima.* Thin-walled vegetative cells from a non-pigmented, 25-day-old, single cell colony. Unstained. (1200x).

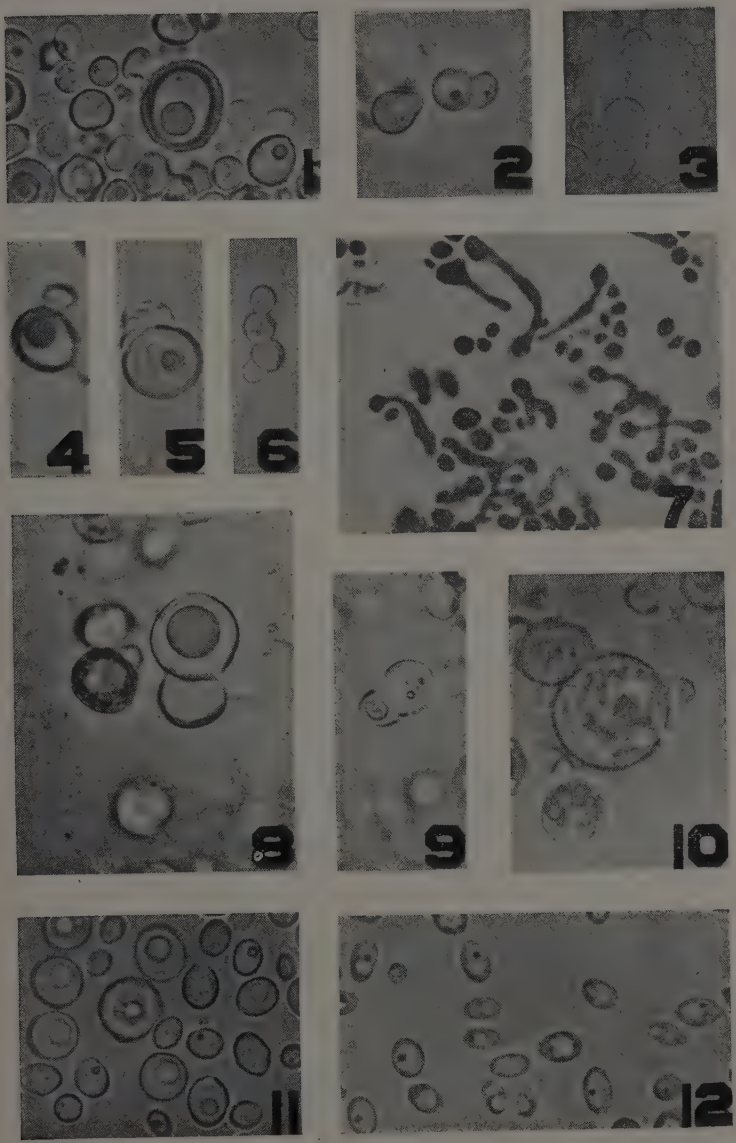


PLATE II

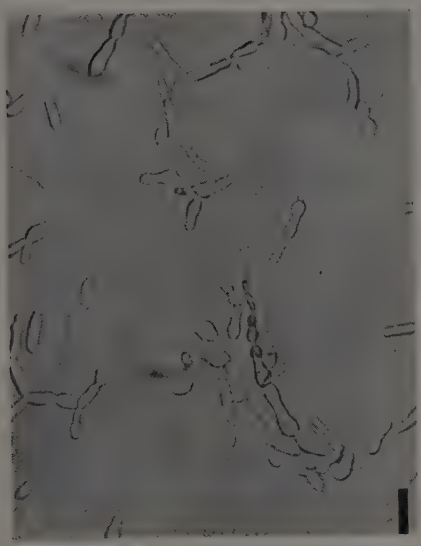
EXPLANATION OF PLATE III

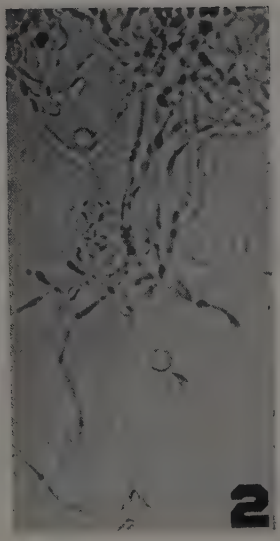
Fig. 1. *T. deformans*. Mycelial tendency occurring in a 2-month-old, single spore, smooth colony. Unstained. (588x).

Fig. 2. *T. deformans*. Mycelial tendency occurring in a rough sector of a 3-month-old, single cell colony. Stained with cotton blue in lactophenol. (588x).

Fig. 3. *T. pulcherrima*. Nuclear staining of cells from a 5-day-old, pigmented, mass culture. (1200x).

Fig. 4. *T. pulcherrima*. Nuclear staining of cells from a 5-day-old, non-pigmented, single cell culture. (1200x).





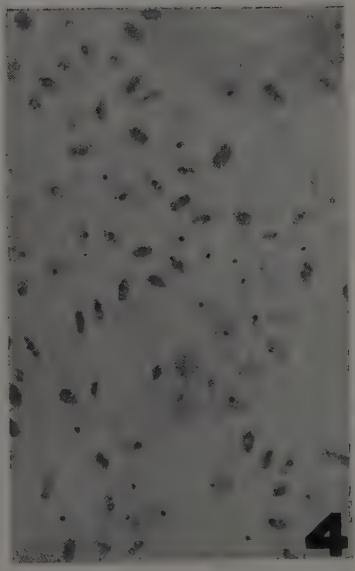


PLATE III

2(3):385–437 FARLOWIA JANUARY, 1946

THE CYPERICOLOUS AND JUNCICOLOUS SPECIES OF SCLEROTINIA

H. H. WHETZEL [1]

During the spring and summer of 1930 I took the opportunity afforded by sabbatic leave to collect and study species of the *Sclerotiniaceae* in Europe. My travels carried me through England, Holland, Switzerland, France, Germany, Denmark, Sweden and Norway. Through the kind co-operation of colleagues [2] in these countries I was enabled to make invaluable collections and studies of many species in their natural habitat. I was also afforded every courtesy and assistance in the examination of specimens of these cup fungi preserved in the herbaria of most of the important botanical institutions in the countries visited.

Stimulated by my early studies on the species of *Sclerotinia* found in northeastern United States on species of *Carex* (Whetzel 1929) I took special pains to collect and study the species of this genus occurring on sedges and rushes in western Europe. I was exceptionally fortunate in finding in nature most such species recorded by European mycologists.

A manuscript presenting the results of my studies on these species was partially prepared during my stay in Europe. On my return, teaching duties prevented the completion of this paper, and only recently have I been able to take up the work again and complete the studies which are here presented. This delay has not been without its compensations in certain respects. During the years that have passed, while much of the freshness and some of the details of my European observations have faded

[1] This manuscript was received and edited before Professor Whetzel's death on November 30, 1944. Realizing that he might not live to see the appearance of his paper, the author made all arrangements for its publication, including a generous gift to cover the extra cost of the halftone plates.

[2] *Acknowledgments:* The researches on which this paper is based, especially those undertaken in Europe in 1930, were made possible largely by grants from the Heckscher Foundation for the Advancement of Research at Cornell University. I am especially indebted to Dr. Cynthia Westcott, who as my research assistant gave invaluable help on my European trip. For access to herbarium specimens and for expert advice and assistance I am greatly indebted to Drs. David H. Linder and W. L. White of the Farlow Herbarium; to Dr. John A. Stevenson of the U.S.D.A.; to Dr. W. G. Solheim of the University of Wyoming; to Dr. J. Ramsbottom of the British Museum; to Dr. A. D. Cotton and Miss E. M. Wakefield of the Royal Herbarium, Kew; to Dr. J. A. Nannfeldt, University of Upsala; and to Mr. Ernst Gram, Dr. C. Ferdinandsen, and Mr. Johs. Grøntved of the University of Copenhagen. My best thanks are also due Miss Charlotte Dill and Mr. Carlos Garcés for preparation of the drawings for the text figures and to Dr. Rolf Singer of the Farlow Herbarium who has kindly prepared the Latin descriptions. Mr. W. R. Fisher prepared the photographs. The writer is indebted to so many other friends and colleagues both in this country and in Europe for assistance and favors that it is useless to attempt to list them all here. To everyone who has thus contributed to the consummation of these investigations I here express my thanks and gratitude.

from my memory, there have come to hand, now and then, specimens and information on species of this group that have corrected some of my earlier conclusions, confirmed others, and have added three species to those known to me at the time of my 1930 visit in Europe.

THE GENUS SCLEROTINIA

The generic name, *Sclerotinia*, should be restricted to those species in which the apothecium arises from a tuberoid sclerotium as in *S. sclerotiorum* (Lib.) De Bary, which is to be taken as the type of the genus. In this genus the sclerotia originate and develop upon the surface of the substrate or in lysigenous cavities within the organs of the suscept. They rarely and only incidentally enclose in their pseudoparenchyma bits of the tissue of the suscept. The sclerotia when freely formed upon the surface of the substratum are approximately loaf-shaped or globose. Even those species which form characteristically shaped sclerotia regularly within the organs of their suscepts, when grown on artificial culture media produce sclerotia which tend to be globose in shape. None of them are true parasites. They must kill the cells of the invaded tissues before they are able to extract the nourishment they seek. They are necrogenic saprophytes. They have no conidial stage. All have spermatia (microconidia) produced endogenously from the tips of obclavate spermatophores, fasciculately massed into mucilaginous spermodochia, borne free on the aerial mycelium or enclosed in lysigenous cavities in the tissues of the suscept.

The species here discussed are the only ones known to me on sedges and rushes that may be properly referred to the genus *Sclerotinia* as above characterized. A number of species of Discomycetes, recorded on various species of these plants and referred to the genus *Sclerotinia*, do not qualify. These in so far as they are known to me are listed and briefly discussed at the end of this paper.

SPECIES TREATED IN THIS PAPER

As a stimulus to the reader to plunge into the details of my observations and conclusions on the species treated in this paper, it may be well to present here a list of these together with the sedges and rushes which they inhabit. There are ten species occurring on forty-one different suscepts. These species are largely restricted each to a distinct suscept or set of suscepts. Only among the four species on *Carex* have there been found a few cases of suscepts common to two or more.

On the Cyperaceae:

1. **Sclerotinia duriaeana** [3] (Tul.) Rehm in EUROPE only. on *Carex brizoides* [4] L.; *C. paniculata* L.; *C. disticha* Huds.; *C. chordorrhiza* Ehrh.;

[3] Exercising his option under the rules, the author decapitalizes the first letter of species names.

[4] The species names here used for the suscepts have been carefully checked by my colleague Dr. R. T. Clausen.

C. acutiformis Ehrh. 2. **Sclerotinia sulcata** (Desm.) Whetzel in EUROPE on *Carex hudsonii* A. Bennett; *C. vulpina* L.; *C. gracilis* Curtis; *C. inflata* Huds.; *C. brizoides* L.; *C. nigra* (L.) Reichard; *C. disticha* Huds.; *C. paradoxa* Willd.; *C. paniculata* L.; *C. riparia* Curtis, in NORTH AMERICA on *Carex stricta* Lam.; *C. prairea* Dewey; *C. interior* Bailey; *C. hystricina* Muhl.; *C. riparia* var. *lacustris* (Willd.) Küken; *C. flava* L.; *C. inflata* var. *utriculata* (Boott) Druce; *C. crinita* Lam.; *C. nebraskensis* Dewey. 3. **Sclerotinia longisclerotialis** Whetzel in NORTH AMERICA only, on *Carex prairea* Dewey; *C. interior* Bailey; *C. vesicaria* L.; *C. crinita* Lam.; *C. retrorsa* Schw.; *C. oligosperma* Michx. 4. **Sclerotinia caricis-ampullaceae** Nyberg in EUROPE and NORTH AMERICA on *Carex aquatilis* Wahl.; *C. aquatilis* var. *altior* (Rydb.) Fern.; *C. inflata* Huds. 5. **Sclerotinia vahliana** Rostr. in EUROPE and NORTH AMERICA on *Eriophorum scheuchzeri* Hoppe; *E. angustifolium* Roth.; *E. vaginatum* L. 6. **Sclerotinia scirpicola** Rehm in EUROPE only, on *Scirpus lacustris* L. 7. **Sclerotinia schoenicola** n.sp. in EUROPE only, on *Schoenus nigricans* L.

On the Juncaceae:

8. **Sclerotinia curreyana** (Berk. *in* Currey) Karst. in EUROPE only, on *Juncus effusus* L.; *J. conglomeratus* L.; *J. glaucus* Ehrh.; *J. filiformis* L.; *J. communis* E. Mey. 9. **Sclerotinia juncigena** (E. & E.) n.comb. in NORTH AMERICA only, on *Juncus effusus* L. var. *pacificus* (Fern.) Wieg. 10. **Sclerotinia luzulae** n.sp. in EUROPE only, on *Luzula pilosa* Willd.

LIFE HISTORY

The life histories of the *Sclerotinia* species attacking sedges and rushes are in their main features very much alike. The discharged ascospores, carried by air currents, fall upon the flowers of their suscepts. Germination and invasion of the flowers is followed promptly by death and browning of the entire inflorescence, the affected culms never setting seed. The invading hyphae now work rather slowly down the culm forming spermodochidia [5] (Text Figs. A, C, D) in the cortical tissues just beneath the epidermis. The increasing mass of spermatia in these fruit bodies soon burst through the epidermis in pearly white or brownish mucilaginous drops. Rain or dew and possibly insects disseminate the spermatia to the surfaces of the dying culms below wherein the sclerotia are now beginning to develop. The mechanism of fertilization is unknown but that the spermatia do function is certain. The sclerotia, at first evident as white soft cottony masses within the culm, gradually harden, enveloping the medulla in a thin black rind. This medulla is often pink at first, eventually becoming white. In the final stages of maturity in late autumn, the sclerotia usually burst the confining outer tissues of the culm. In some species they fall out of the culms onto the water or moss beneath. In other species they remain partially enclosed,

[5] For a definition of this term see Whetzel, Mycologia **35:** 335–338. 1943.

exposing only a part of their surface. In one species, *S. longisclerotialis* (Fig. 20), the sclerotia remain enclosed until decay of the culm tissues more or less frees them the following spring. The natural shape of the sclerotium is usually characteristic for each species, but is evidently determined to some extent by the shape of the enveloping culm. The number of sclerotia per culm varies not only with the species of *Sclerotinia* but to some extent, and within limits, in most of the species of their respective suscepts.

The sclerotia of those species in which they are freed at maturity, float on the surface of the water, eventually finding lodgment among the mass of debris about the hummocks or shores of the swamp. In some species the sclerotia remain upright in the dead culms throughout the winter. In *S. longisclerotialis* the dead slender culms enclosing the sclerotia fall over and settle to the bottom of the pools about the hummocks.

Development and maturity of the apothecia of all the species are closely correlated with the growth and flowering of their respective suscepts early in the spring. The ascospores are matured and discharged over a period of two weeks or so while the flowers of their suscepts are opening and shedding their pollen. Thus for the species of *Sclerotinia* attacking sedges and rushes there is a single primary cycle of activities. So far as known, secondary cycles do not occur. Each species presents certain peculiarities and variations from the life-history picture outlined above. These will be pointed out in connection with the discussion of the different species. This outline of their life history is inferred largely from observations on their seasonal developments and the syndrome of the diseases they cause. Most of them have been grown on potato dextrose agar. Much remains to be discovered by further field studies and especially by carefully executed inoculation experiments. Several of them, no doubt, have a more extensive suscept range than my observations indicate. They appear to have been very infrequently collected, not only in North America but also in Europe. Considering their abundance and annual reappearance in the localities where I have had them under observation, it is surprising how scanty in numbers and quantities are the specimens in the herbaria which I have visited.

SPECIES ON THE CYPERACEAE

Of the seven species of *Sclerotinia* known to me to attack members of the *Cyperaceae*, four occur on species of *Carex*, one on *Scirpus*, one on *Eriophorum*, and one on *Schoenus*. These appear to constitute a group of very closely related species. All occur in much the same type of environment, namely in wet marshes where water stands throughout the year or along the margins of lakes, ponds, and quiet streams. They appear to be restricted to the cooler parts of the north temperate zone and on up into the colder arctic regions. They usually occur in great abundance in the localities where I have found them both in America and Europe.

SPECIES ON CAREX

Four species of *Sclerotinia* pathogenic to *Carex* species have been described. Of these *S. duriaeana* (Tul.) Rehm is known only from northwestern Europe, occurring widely on several species of *Carex* from France northward to Lapland in Scandinavia; *S. sulcata* (Desm.) Whetzel occurs in both Europe and America. It appears to be generally distributed over western Europe from south to north wherever its *Carex* suscepts occur. It is this species which has been most frequently collected and preserved in European herbaria but almost always erroneously labeled *Sclerotinia duriaeana*, with which it has generally been confused by European mycologists. While *S. longisclerotialis* Whetzel infects many species of *Carex* in northeastern United States it apparently does not occur in Europe. The fourth species, *S. caricis-ampullaceae* Nyberg, discovered in Finland in 1930 and first described two years later, has been collected since in Sweden as well as in North America in the high mountain swamps of Wyoming (Whetzel and Solheim 1943). This is the largest and most striking of the four species (Fig. 25). The apothecia of these four species differ chiefly in size and somewhat in shape. The differences in color of the apothecia and in the shape and size of asci and ascospores are scarcely of taxonomic significance. The species are most clearly distinguishable by the shape and size of their sclerotia together with the external appearance and arrangement of their spermodochidia.

KEY TO THE SPECIES

1. Sclerotia short, more or less fusiform, falcate or kidney-shaped.
   2. Spermodochidia in globose, equally spaced groups..... **S. duriaeana**
   2. Spermodochidia in linear, scattered groups..... **S. sulcata**
1. Sclerotia long and slender.
   3. Sclerotia of uniform diameter, truncate, more or less 3-angled **S. longisclerotialis**
   3. Sclerotia obclavate, drawn out above into a slender whiplike tip **S. caricis-ampullaceae**

SCLEROTINIA DURIAEANA

PLATE I & II

A clear and accurate concept of this species has long been beclouded by errors in identification of certain stages in its development and by its frequent confusion with *S. sulcata* (Desm.) Whet. by mycologists subsequent to its description by Tulasne in 1861. I have already presented (Whetzel 1929) in some detail the basic evidence for this confusion of the two species. Critical examination of specimens preserved in European herbaria together with observations in the field, in culture, and on preserved specimens of both these species personally collected on numerous species of *Carex* in Europe during 1930, has fully confirmed my earlier provisional conclusion (Whetzel 1929: 15) that the two species have commonly been confused under the name *Sclerotinia duriaeana*.

While I made numerous collections of the spermatial and sclerotial stages of this species in most of the countries visited, I was in most places too late

PLATE I

to find apothecia. Unfortunately I was unable to visit the type locality where Durieu made his collections and observations on this species. I did, however, make two collections of apothecia which appear to be those of *S. duriaeana*, one near Rambouillet, France, (CUPP *31561*) and another near Lyngby, Denmark, (CUPP *31564*) (see data and comments below p. 395). In neither case were many apothecia found and the circumstances under which they were taken raises some question as to their identity. Perhaps if I had found abundant fresh cups of both species, each of unquestionable identity, I might have detected some differences of specific significance in their apothecia. I doubt it. Such evidence as is available offers little expectation that they are thus distinguishable. The sclerotia of the two species cannot with confidence be told apart and the spermatial stages alone provide ready and certain identification. (Compare Figs. 1 and 13.) A more extensive comparison than I have been able to make of these two species in artificial pure culture would almost certainly also provide dependable evidence for distinguishing between them.

In view of the scattered, confused and incomplete published data and descriptions of *S. duriaeana*, it appears desirable to present here a more complete and accurate description of the species, interpreted in the light of my own studies and observations.

SCLEROTINIA DURIAEANA (Tul.) Rehm, Hedwigia **21:** 66. 1882.

Epidocium ambiens Desm. Ann. Sci. Nat. Ser. 3, **20:** 231. 1853.
Peziza duriaeana Tul. Sel. Fung. Carp. **1:** 103. 1861, and **3:** 203, *pl. 22, fig. 20–24.* 1865.
Sphacelia nigricans sensu Sacc. Michelia **2:** 131. 1880.
Sclerotium nigricans sensu Sacc. Michelia **2:** 134. 1880.
Sphacelia ambiens Sacc. Syll. Fung. **4:** 666. 1886.
Sclerotinia duriaeana Sacc. Syll. Fung. **8:** 199. 1889.
Sclerotinia duriaeana (Tul.) Quélet (In error. See Notes p. 395.)
Hymenoscypha duriaeana Phill. Manual Brit. Discom. p. 115. 1893.
Myrioconium ambiens V. Höhnel. Mitt. Bot. Inst. Tech. Hochsch. Wien. **3:** 50. 1926.

Spermodochidia (Figs. 1, 3 & 7) dull black in paired groups of 3–6 at regular intervals of 5–15 mm. along upper part of culm, 5–15 paired groups per culm, groups oblong to subglobose when moist, 1–3 mm. long, arranged parallel side by side lengthwise of the culm, usually on but two sides of the 3-angled culm, sometimes encircling the culm as in *C. chordorrhiza* (Fig. 2); at maturity becoming swollen and rupturing the culm, discharging the viscid, olivaceous mass of spermatia; *spermatia* minute, globose, 2–3 μ in diam., faintly olivaceous.

The spermodochidia are formed in lysigenous cavities in the palisade parenchyma of the culm, between the vascular bundles. Each spermo-

Plate 1. *Sclerotinia duriaeana.* **Fig. 1.** (Left) diseased heads of *Carex paniculata* L.; (right) healthy head, with spermodochidia and sclerotia in the diseased culms. CUPP *31562.* **Fig. 2.** Diseased culms of *C. chordorrhiza* Ehrh. showing the spermodochidia. CUPP *31563.* **Fig. 3.** Culm of *C. paniculata* with spermodochidia and sclerotium from De Thümen's Myc. Univ. *1557.* All figures natural size.

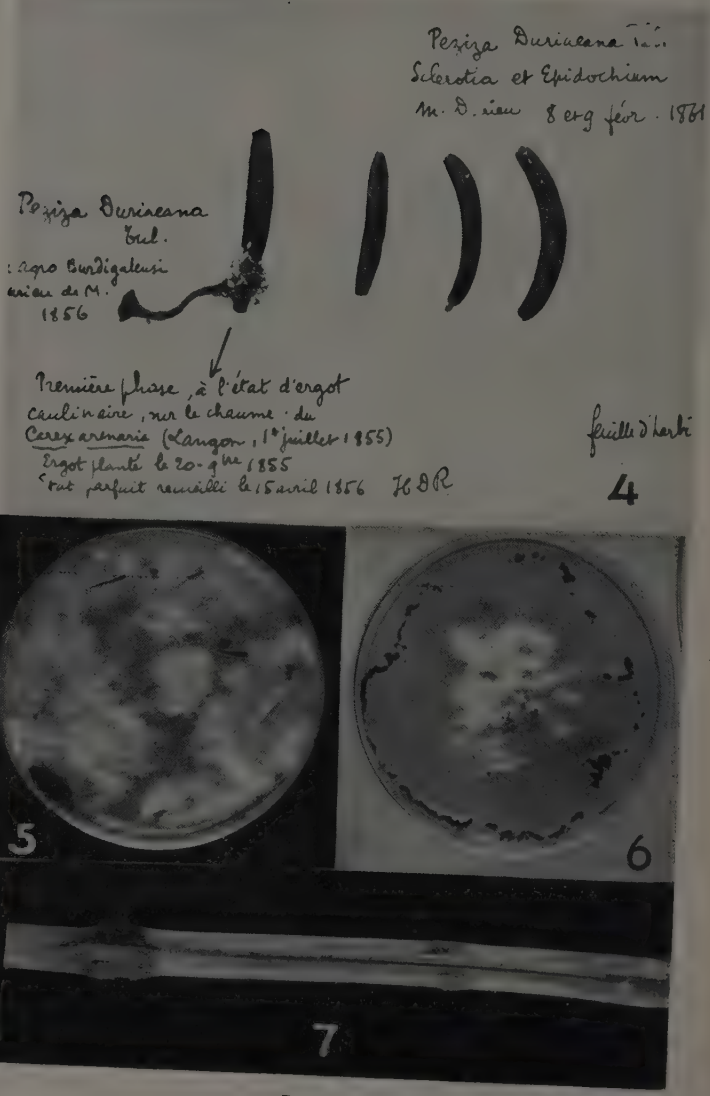

Peziza Duriaeana Tul.
Sclerotia et Epidochium
in D. ieu 8 erg fév. 1861
Peziza Duriaeana
Tul.
: Agro Burdigalensi
ariau de M.
1856
Première phase, à l'état d'ergot
caulinaire, sur le chaume du
Carex arenaria (Langon, 1er juillet 1855)
Ergot planté le 20-9bre 1855
État parfait recueilli le 15 avril 1856 HDR
feuille d'herb
4
5
6
7

PLATE II

dochidium contains many spermodochia surrounded by masses of spermatia. (See Tulasne 1865: *pl. 22, fig. 21.*)

Sclerotia (Fig. 4) one to several in each culm, from which they are discharged at maturity through a slit in the culm over the sclerotium by the toppling of the upper part of the culm which bending at this point opens the sclerotial cavity; black, slender, fusiform, more or less curved when dry, when fresh plump, fusoid, slightly 3-angled, varying in length and thickness according to the size of the culm in which formed, 5–15 mm. long. The sclerotia first appear within the culm as elongate, pink, cottony masses of hyphae, which gradually darken externally as the dull black rind is formed and the densely packed thick-walled hyphae of the white medulla takes form.

Apothecia variable in size, depending upon the size of the sclerotia from which they arise, usually but one from each sclerotium; *cup*, 5–10 mm. in diam. occasionally larger, shrinking greatly on drying, deep goblet-shaped, thin, fragile, light fawn to vinaceous brown, lighter beneath due to a fine hyphal fuzz which covers the under surface when fresh; *stipe* rather short, its length usually about the diameter of the fully open cup, nearly or quite smooth; *asci*, according to Tulasne (1861: 106) are "8-spored (spores obliquely and closely uniseriate, seldom biseriate), cylindrical, obtuse, straight, 8–9.5 μ wide and about ten times as long." Boudier (1910: 274) describes them as cylindrical, rather large, slightly attenuate toward the base, 8-spored, pore blue with iodine, 210–230 x 7–10 μ; *ascospores* are described by Tulasne (*l.c.*) as "ovate, inequilateral, obtuse at both ends and muticous, smooth, unilocular, and filled with oil the greater part measuring 10–15 x 6.5–7.5 μ, but some not exceeding 8–9.5 x 5 μ." Boudier describes them as oblong-fusiform, colorless, usually without internal granules, but sometimes cloudy or rarely with non-oily droplets, 14–18 x 6–7 μ. Tulasne (1865: *pl. 22, fig. 24*) describes the discharge of the ascospores and their germination which he illustrates showing the direct formation on them of spermatophores and spermatia; *paraphyses* slender, slightly thickened at the tips, hyaline, sparingly septate, vacuolate (Boudier 1907: *pl. 473, fig. 9*; 1910: 274).

. HABITAT: In culms of *Carex* species, growing in open swamps, marshes and wet meadows in western Europe.

TYPE SPECIMENS: Collected by Durieu de Maisonneuve in culms of *Carex brizoides* L. during the years 1855 to 1861 in the sandy meadows along the river Ciron about the ruins of the Château de Fargues not far from the towns of Langon and Bazas, France. There appears to be no

Plate 2. *Sclerotinia duriaeana.* **Fig. 4.** Photograph of Durieu's type specimens of the apothecium and sclerotia deposited in the Botanical Museum, Paris, sent me by Roger Heim; natural size. Tulasne (Sel. Fung. Carp. **3:** pl. 22, fig. 23) presents a good sketch of the apothecium of this species. **Fig. 5.** Mycelial growth from bits of diseased culms of *C. paniculata* on potato dextrose agar; ½ natural size. CUPP *31562.* **Fig. 6.** Mycelium and spermodochidial masses from tissue plantings from culms of *C. chordorrhiza* on potato dextrose agar; ½ natural size. CUPP *31563.* **Fig. 7.** Spermodochidia on culm of *C. chordorrhiza*, x6. CUPP *31563.*

evidence that Tulasne preserved specimens of the materials on which his description of the species was based. The specimens he had in hand appear to have all been sent him by Durieu. Durieu, however, preserved what are obviously duplicate specimens of those sent Tulasne. These specimens were later, 1878, deposited in the cryptogamic herbarium of the Museum of Natural History in Paris (Fig. 4). These specimens therefore may be properly considered the type specimens of this species. These, together with rather extensive notes in Durieu's handwriting, were in 1930 mounted on herbarium sheets. Photographic copies of three of these sheets were kindly sent me by the curator, Dr. Roger Heim, after my visit to the museum. These are on file with my notes on this species. Duplicate specimens of sclerotia and infected inflorescences bearing spermodochidia from Durieu's collection of June 24 and 26, 1860, are filed in CUPP *17044*. I found among Durieu's specimens but one apothecium (Fig. 4), apparently one of those developed from his first collection of sclerotia, July 1, 1855.

Since no species of *Carex* other than *C. brizoides* was found in Durieu's collections, and since this is the species pictured by Tulasne, it would appear that neither of them had in hand specimens of *S. sulcata* which they might have confused with *S. duriaeana*. Tulasne's (1861: 103) application of the name *Sclerotium sulcatum* Roberge *in* Desmaz. to the sclerotial stage of *S. duriaeana* was at the time a pardonable error. The only other name of the sclerotial stage of this species which has been applied is *Sclerotium nigricans* Sacc. given it by Saccardo (1880: 134, and 1899: 1153) under the erroneous impression, however, that the specimens in hand were sclerotia of *Claviceps nigricans* Tul.

DISTRIBUTION: This species is known to occur only in Europe. It has not been found in North America. Apothecia apparently appearing in May, spermodochidia June to July, sclerotia July and August. It is known to me from France, Belgium, Germany, England, Denmark and Norway.

ILLUSTRATIONS: Tulasne, Sel. Fung. Carp. **3,** *pl. 22, fig. 20–24.* 1865. Boudier, Icon. Myc. **3:** *pl. 473.* 1907.

MATERIAL EXAMINED: On **Carex brizoides** L. (*C. arenaria* in error): (1) Durieu's type specimens deposited in the Crypt. Herb. Mus. Nat. Hist., Paris (fully discussed above). I also found what appear to be duplicate specimens (spermodochidia and sclerotia) from Durieu's collections in the Kew Herbarium labeled "*Peziza Duriaeana* on *Carex arenaria*" from Cooke's herbarium; — (2) Krieger, Fung. Sax. *1682*, "am grossen Winterberg," Germany, August 1, 1898 (spermodochidia and sclerotia). On **Carex paniculata** L.: Desmazières, Pl. Crypt. France. Ser. II, **20,** "Epidocium ambiens Desm. Not. XXI. En été, sur les tiges sèches de divers Carex, à Ouystreham par M. Roberge." France (spermodochidia only); — De Thümen, Mycotheca Univ. *1575*, "Epidocium ambiens Desm. f. Caricis paniculatae. Gallia. Grande Chartreuse pr. Grenoble. Aug. 1879, J. Therry." (spermodochidia and sclerotia); Roumeguère, Fungi Sel. *4682* "Sphacelia ambiens (Desm.) Sacc." (spermodochidia only); his Fungi Gallici *1200*, "Sclerotium nigricans (Tul.) Sacc." (spermodochidia) all appear to have been made up from one and the same original collection by Therry; — Roumeguère, Fungi Gallici *3505*, "Epidocium affine Desm. 3N.21. Chaumes du Carex paniculata. Tremonde (Belgique). Reliq. Westendorp." This is incorrectly determined. It is typical *Epidocium ambiens* Desm. The spermodochidia (no sclerotia) are typical of those of *S. duriaeana.* No date of collection is given; — Roumeguère, Fungi Sel. *4600*, "Sclerotium sulcatum

Rob. A l'interieur des chaumes secs du Carex paniculata. Louette Saint Pierre (Belgique). legit Aubert." (sclerotia only). No date given; — CUPP *31561*, swamp near Rambouillet, France, May 6, 1930, *Whetzel, Westcott & Duffrenoy*. Several apothecia found lodged on hummocks of *Carex paniculata* standing in a pool of water. It is barely possible that some of these apothecia are those of *S. sulcata*. Ascospores discharged from two of them (Figs. 5, 6) gave, however, cultures quite different from cultures of *S. sulcata* (Figs. 17, 18) and like those from infected culms of the following collection; — CUPP *31562*, swamp in outskirts of Faaborg, Isle of Fyn., Denmark, June 27, 1930, *Whetzel & E. Gram* (spermodochidia and sclerotia). On **Carex disticha** Huds.: Roumeguère, Fungi Selecti. Exs. *5419*, "Sclerotinia Duriaeana Tul. (conidies). Sur les chaumes maladifs d'un Carex sp. King's Lynn (Angleterre), Automne 1889." Coll. Plowright (sclerotia and spermodochidia). A. J. Wilmott of the British Museum says the *Carex* is *C. disticha* Huds.; — Phillips Herbarium, Brit. Mus., three collections on one sheet. One is labeled "Peziza Duriaeana Tul. King's Lynn. July 1888," presumably collected by Plowright, showing typical spermodochidia. A. J. Wilmott identified the suscept as *Carex disticha* Huds. Two others are sclerotia which bear apothecia, labeled respectively: "Peziza Duriaeana Tul., growing from sclerotia gathered June 3, 1883 by C. B. Plowright, King's Lynn"; and "Peziza Duriaeana Tul. cultivated from sclerotia on *Carex arenaria* by C. B. Plowright, June 1, 1883." Dupl. in CUPP *33271*. On **Carex chordorrhiza** Ehrh.: Flora Suecica, *1636*, under the name *Myrioconium ambiens* (Desm.), the spermatial stage only. Collected by J. A. Nannfeldt in Torne Lappmark, Jukkäsjarvi, at Abisko above the railway station August 9, 1928. Dupl. in CUPP *31620*. Apparently the first collection on this suscept; — CUPP *31563*, marshy bogs near hotel at Fjellsäter above Trondhjem, Norway. July 8, 1930, *Whetzel & Jørstad* (spermodochidia and sclerotia). On **Carex acutiformis** Ehrh. (?) (new suscept): CUPP *31564*, along the shore of Lyngby Sö, Lyngby, Denmark. June 5 and June 17, 1930, *H. H. Whetzel* (apothecia and sclerotia). The determination of the suscept by Grøntved of the University of Copenhagen is in some doubt as the single culm enclosing sclerotia is old and rotten.

In making the transfer of this species to the genus *Sclerotinia*, Rehm had before him (his Ascomyceten *603*) specimens of *S. sulcata* which he mistakenly took to be those of Tulasne's species *Peziza duriaeana* (Whetzel 1929: 7).

The combination, *Sclerotinia duriaeana* (Tul.) Quél. appears to be a strange error, originally made by Rehm in his "Discomyceten" *in* Rabenh. Krypt. Flora **1**[3]: 820. 1893. He here lists this species as "*Scl. Duriaeana* (Tul)" giving as a synonym, "Sclerotinia Duriaeana Quél. Bull. soc. myc. I. pag. 115". An examination of this reference discloses that the paper is by Boudier (not Quélet) in which he merely lists "*P*[*eziza*] *Duriaeana* Tul." as an example of species to be included in *Sclerotinia* Fckl. which Boudier makes a sub-genus of *Ciboria* Fckl. Later Boudier in his Icones Myc. **4:** 274 writes "*Sclerotinia Duriaeana* (Tul.) Quél." without citing the place where Quélet is assumed to have made the transfer. Succeeding authors appear to have perpetuated the error.

Massee (1895: 283) cites as a synonym of *Sclerotinia duriaeana*, "*Epidocium arabicus* Desmaz. xxii. Not. in Ann. Sci. Nat., p. 19." This species name appears to be a strange error in the spelling of the name "*ambiens*." The reference he gives is obviously that of the original place of publication of *Epidocium ambiens*, the page being apparently that of a reprint instead of the original.

The names *Sphacelia nigricans* and *Sclerotium nigricans* were erected by

Saccardo who erroneously believed the sclerotia and spermodochidia in specimens (of *S. duriaeana*) on *Carex paniculata* were the sclerotia and spermoidea of *Claviceps nigricans* Tul. (Whetzel 1929: 9–10 and 1944: 426–428).

Von Höhnel (1926a: 50–51) erroneously lists *Epidocium affine* Desm. as synonymous with his *Myrioconium ambiens*, believing it to be the same as or a variety of *Epidocium ambiens* of Desmazières.

There is considerable variation in the measurements of asci and ascospores of *S. duriaeana* as recorded by different authors. I have made measurements of asci and ascospores from three collections of apothecia with the following results: (1) Plowright's collection on *C. paniculata:* asci (6 meas.) 121.2–151.5 x 6–9.5 μ; spores (50 meas.) 9.9–18.4 x 4.6–6.6 μ, mode 12.5 x 5.3 μ, av. 12.7 x 5.4 μ. (2) Whetzel's collection on *C. paniculata* (CUPP, *31561*): asci (30 meas.) 133.3–181.8 x 8.1–10.8 μ, mode 157.5 x 8.1 μ, av. 158.9 x 8.3 μ; spores (50 meas.) 10.5–14.5 x 4.6–7.2 μ, mode 11.8 x 5.3 μ, av. 11.9 x 5.4 μ. (3) Whetzel's collection on *C. acutiformis* (CUPP, *31564*): asci (40 meas.) 127.2–169.6 x 8.1–9.5 μ, mode 151.5 x 8.1 μ, av. 147.6 x 8.7 μ; spores (80 meas.) 9.9–15.8 x 5.3–7.9 μ, mode 13.2 x 6.6 μ, av. 13.3 x 6.5 μ. These measurements are distinctly smaller than those given by Boudier, but compare favorably with those given by Tulasne.

Although I cite Boudier's description and illustrations which he presents under the name *S. duriaeana*, I do so with some reservations. He does not specify the species of *Carex* on which his specimens occurred. His illustrations might just as well be those of *S. sulcata*. His measurements for asci and ascospores are rather large in comparison with the measurements of asci and spores of *S. duriaeana*. They more nearly approximate the maximum measurements of these structures in *S. sulcata*.

Whoever was responsible (presumably Durieu) for the identification of the *Carex* harboring the *Peziza duriaeana* which Tulasne had in hand, appears to have been in error. Culms from these collections bearing the typical spermodochidia and sclerotia as pictured by Tulasne (1865: *pl. 22, fig. 20*) have been critically examined by competent European taxonomists and declared to be *Carex brizoides* L., not *C. arenaria* L.

It is to be noted that of the *Carex* species on which *S. duriaeana* is known to occur only two are reported from North America. This may account for its apparent absence from the Western Hemisphere. It would appear to be most common and widely occurring on *Carex paniculata* and may yet be found on this suscept where that occurs in the Western Hemisphere.

SCLEROTINIA SULCATA

PLATES III AND IV AND TEXT FIG. A

This species is apparently the most common and widely distributed of the *Sclerotinia* species on *Carex*. It occurs throughout northwestern Europe, northeastern United States and in the Pacific Northwest. Long confused with *S. duriaeana*, its distinct identity was first suggested by the writer (Whetzel 1929: 15). In this paper I reviewed in some detail the evidence

then available to me. My study of the species in Europe in 1930 has fully confirmed that conclusion. In that paper (*l.c.*: 19–24) I described it under the name *Sclerotinia duriaeana* ("affine form"), but anticipating the correctness of my belief that it was a species distinct from *S. duriaeana* I made the combination *S. sulcata* (*l.c.*: 15). It is here again briefly characterized under its proper name.

SCLEROTINIA SULCATA (Desm.) Whetzel, Mycologia **21:** 15. 1929.

Sclerotium sulcatum Roberge *in* Herb. Desm. (in part) Ann. Sci. Nat. Ser. 3, **16:** 329. 1851.

Epidochium affine Desm. (in part) Ann. Sci. Nat. Ser. 3, **20:** 232. 1853.

Claviceps (?) *caricina* Griffiths, Bull. Torrey Club **29:** 300. 1902.

Sclerotinia duriaeana "ambiens form," Whetzel, Mycologia **21:** 15. 1929.

Spermodochidia (Figs. 8–14) scattered irregularly along the upper part of the affected culm, usually confined to that part above the first sclerotium, sometimes a few below between sclerotia; almost always confined to two faces of the 3-angled culm; distinctly linear, 2–5 mm. long by ⅓ to ½ mm. broad; dull olivaceous brown, inconspicuous especially in dry culms, splitting longitudinally when mature to release the spermatial ooze. Their structure is illustrated in Text Fig. A; *spermatia* globose about 2 μ in diam., hyaline, produced endogenously and in succession from the tips of densely clustered obclavate spermatophores, embedded in a mucilaginous matrix.

Sclerotia (Fig. 16) one to three in each culm, fusiform, ends blunt, rounded, sulcate, at first pink, then smoky gray and finally black, variable in size, depending on the slenderness of the culm in which formed, 20–25 mm. by 3–4 mm. in the large culms of *C. riparia* var. *lacustris*, 4–5 mm. by 1½–2 mm. in *C. interior*. (For a more detailed description see Whetzel 1929: 20.)

Apothecia (Fig. 15) usually but one from each sclerotium, short-stipitate, fawn-colored; *cups* deep goblet-shaped to shallow funnel-shaped when fully expanded, varying in size from 2 to 10 mm. broad, about half as deep, smooth without, membranous; *stipe* relatively short, 5–20 mm. long, smooth and concolorous with cup above, darker below; *asci* slender, clavate, apex rounded, pore J+, 8-spored, spores uniseriate, 106 meas. of asci from 6 apothecia from *C. stricta* 128–183 x 7.3 x 11 μ, mode 155.8 x 9.16 μ, av. 161 x 8.6 μ; *ascospores* hyaline, ovoid, more or less inequilateral, 205 meas. from 5 apothecia from *C. stricta* 8.8–17.5 x 5.3–8.8 μ, mode 13.1 x 7.09 μ, av. 12.6 x 6.9 μ; *paraphyses* slender clavate, hyaline.

HABITAT: In culms of *Carex* species in swamps, wet, open marshes and along banks of slow streams and ponds. Europe and North America.

LECTOTYPE SPECIMEN: Cornell University Pl. Path. Herb. *11515* on *Carex stricta* Lam., McLean, N. Y., swamp just south of Lloyd Preserve. April 26, 1921, *Whetzel*. Duplicate deposited in Kew Herbarium, Kew, England.

DISTRIBUTION: Known to me in North America only from the region about Ithaca, N. Y., Delaware and the Pacific Northwest (Oregon). It will almost certainly be found when sought throughout northern United States

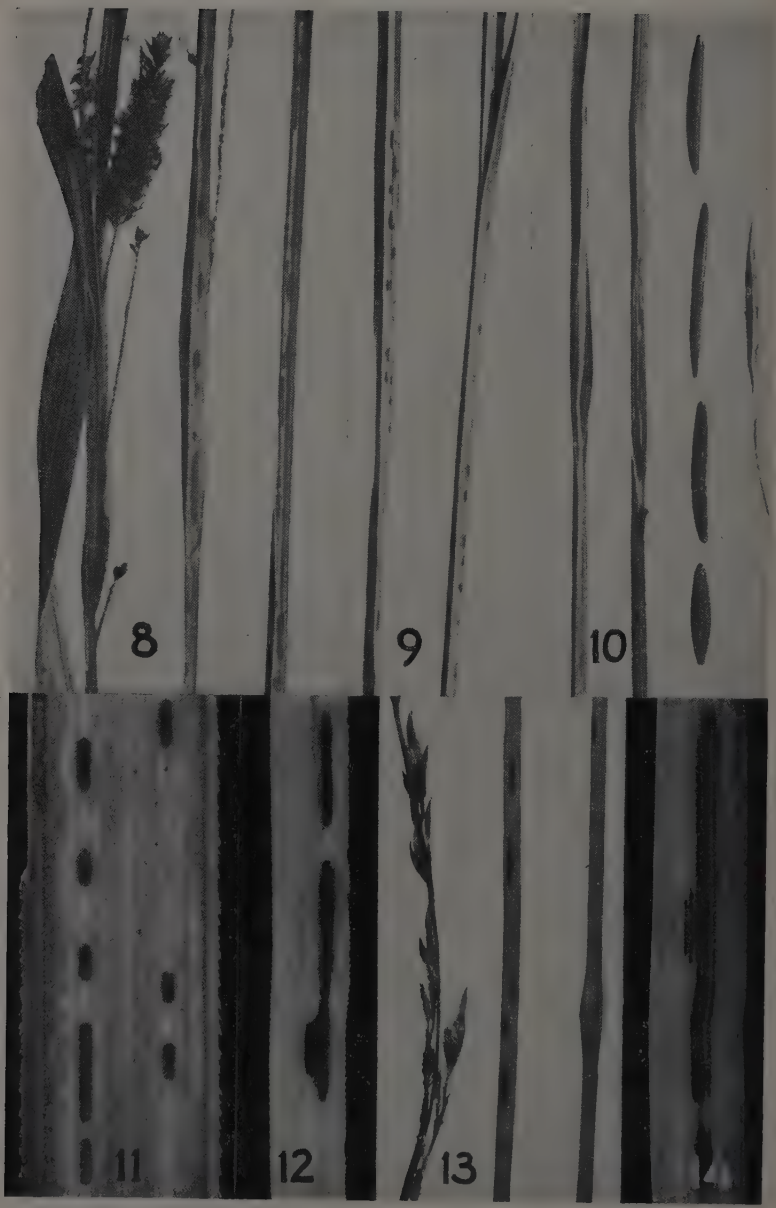


PLATE III

and Canada. It is apparently common throughout northwestern Europe as the records (below) of European specimens examined would indicate. The apothecia appear early in the spring (April–May) at the time the *Carex* suscepts are beginning to flower. The spermodochidia and sclerotia begin to appear about a month later (June–July) and may be readily spotted in the dead bleached culms standing among the healthy.

ILLUSTRATIONS: Whetzel, Mycologia **21:** *fig. 1–7, 14–19,* 1929.

MATERIAL EXAMINED: In connection with my original description of this species (1929) I recorded the North American species of *Carex* then known to me, on which *S. sulcata* occurs. Since that time no additional collections of this species of special interest from North America have come into my hands. To round out the picture I present here the records of European collections which I have examined and studied: On **Carex Hudsonii** Bennett. (=*C. stricta* Good.): Desmazières, Pl. Crypt. France, Ser. II, *21.* "*Epidocium affine*" (spermodochidia only); — Lindhart, Fungi hungarici, *381,* "Peziza Duriaeana Tul." on *Carex,* Hansag, Nov. 1883 (sclerotia and spermodochidia); — Rehm, Ascomyceten, *603 a,* "Sclerotinia Duriaeana (Tul.)" on "Carex stricta Good.", Diessenhofen, Thurgau, Switzerland, Apr. 1881, "Dr. Winter" (sclerotia and apothecia); — Rehm, Ascomyceten, *603 b,* "Sclerotinia Duriaeana (Tul.) Walesellen bei Zürich, Auf faulenden Halmen, Carex stricta, 4/1893. Dr. V. Tavel" (apothecia and sclerotia); — Rabenhorst-Winter, Fungi Europaei, *2749.* "Sclerotinia Duriaeana (Tul.)" on *Carex stricta* Good., Diessenhofen, Switzerland, April 1882, *H. Wegelin* (apothecia and sclerotia); — CUPP *31566,* swamp near Fuer Sö, Jagerhuset, Denmark, June 8, 1930, *Whetzel* (spermodochidia and young sclerotia); — CUPP *31567,* along shore of Sjael Sö, Denmark, June 20, 1930, *Whetzel & Ferdinandsen* (spermodochidia); — CUPP *31568,* swamp on outskirts of Copenhagen, near Söburg, June 21, 1930. *Whetzel & Grøntved* (spermodochidia); — CUPP *31569,* Ryggmossen near Upsala, Sweden, May 28, 1931, *K. G. Ridehies* (apothecia and sclerotia). Dupl. in Herb. Univ. Upsala, Sweden. On **Carex vulpina** L.: Desmazières, Pl. Crypt. France, Ser. I, Ed. 1, *2029* and Ser. I, Ed. 2, *1629.* "Sclerotium sulcatum Rob. in herb." (spermodochidia and sclerotia); — CUPP *31576,* Upper Grimley, brick pits, Worcestershire, England, August 8, 1930, *Whetzel & C. Rea* (spermodochidia). On **Carex gracilis** Curtis: CUPP *31570,* Upton-on-Severn, Worcestershire, England, August 8, 1930, *Whetzel & C. Rea* (spermodochidia and sclerotia); — CUPP *31571,* Upper Grimley, brick pits, Worcestershire, England, August 8, 1930, *Whetzel & C. Rea* (spermodochidia and sclerotia). On **Carex inflata** Huds. (=*C. rostrata* Stokes): CUPP *31572,* swamp in woods at Nosten, parish of Bondhyrho near Upsala, Sweden, July 3, 1930, *Whetzel & Nannfeldt* (spermodochidia). On **Carex brizoides** L.: CUPP *31573,* swamp in woods at Nosten, parish of Bondhyrho near Upsala, Sweden, July 3, 1930, *Whetzel & Nannfeldt* (spermodochidia). On **Carex nigra** (L.) Reichard (=*C. Goodenowii* Gay): CUPP *31574,* swamp in woods at Nosten, parish of Bondhyrho near Upsala, Sweden, July 3, 1930, *Whetzel & Nannfeldt* (spermodochidia). On **Carex disticha** Huds.: CUPP *31575,* along shore of Lyngby Sö, Lyngby, Denmark, June 21, 1930, *Whetzel* (spermodochidia). On **Carex paradoxa** Willd.: CUPP *31578,* swamp near Fuer Sö, Jagerhuset, Denmark, June 24, 1930, *Whetzel & Buchwald* (spermodochidia). On **Carex paniculata** L.: CUPP *31579,* marsh near Faaborg, Isle of Fyn, Denmark, June 29, 1930, *Whetzel & E. Gram* (spermodochidia). On **Carex riparia** Curtis: CUPP *31580,* Knapp's brickyard, Claines, Worcestershire, England, August 7, 1930, *Whetzel & C. Rea* (spermodochidia and

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Plate 3. *Sclerotinia sulcata.* **Figs. 8–10.** Diseased culms of *C. gracilis* showing diseased inflorescence, spermodochidia, and sclerotia; natural size. CUPP *31571.* **Fig. 11.** Spermodochidia on culms of *C. vulpina,* x6. CUPP *31576.* **Fig. 12.** Spermodochidia on culms of *C. paniculata,* x6. CUPP *31579.* **Fig. 13.** Diseased inflorescence, spermodochidia and sclerotia on culm of *C. prairea;* natural size. CUPP *14947.* **Fig. 14.** Spermodochidia on culms of *C. gracilis* x6. CUPP *31571.*

Text Fig. A. Cross section through a spermodochidium of *Sclerotinia sulcata* in culm of *C. paniculata* about x325. Note that the cavity is formed by lysis of the parenchyma between the vascular bundles. Drawn by Carlos Garcés.

sclerotia); — CUPP *31581*, valley of the Avon, south of Salisbury near Woodgreen, Hampshire, England, August 4, 1930, *Whetzel & Wm. Brown* (spermodochidia and sclerotia). On **Carex** sp.: Herbarium of C. Crossland (Herb. Kew, England), "Sclerotinia Duriaeana (Tul.) Quel. Among decaying Carex etc. Masham, (Yorkshire), England. May 28, 1902" (sclerotia and apothecia).

The earliest name applied to any stage of this species is *Sclerotium sulcatum* Roberge in herb. Desm. (1851). Two years later Desmazières described the spermodochidial stage under the name *Epidocium affine*. Both of these names were based on mixtures of culms of *Carex* species and *Schoenus nigricans*, the sclerotia and spermodochidia on the latter, being those of a heretofore undescribed species of *Sclerotinia*. (See p. 421). These stages as well as the apothecia of *Sclerotinia sulcata* were long confused by European mycologists with those of *S. duriaeana*. The writer (Whetzel 1929: 15) appears to have been the first to suspect its specific identity.

The only recorded collection of this species in North America, prior to 1929, as far as I have been able to discover, was made by Griffiths and Morris in August 1901 near Andrews, Oregon on *Carex nebraskensis*. Their collection consists of sclerotia and spermodochidia only. Griffiths (1902) described the fungus under the name "*Claviceps? caricina* sp. nov." Groh (1911) having had occasion to examine this collection by Griffiths and Morris which had been distributed as West American Fungi *400*, referred it to Güssow who identified the fungus as *Sclerotium sulcatum* but erroneously referred the spermodochidia to *Epidocium ambiens*, the spermatial stage of *Sclerotinia duriaeana*.

It would appear from the recorded collections that *S. sulcata* is more common in Europe than *S. duriaeana* and goes to a greater number of *Carex* species. Both species are recorded on *C. brizoides*, *C. paniculata* and *C. disticha*. While *Carex paniculata* and its closely related species, *C. brizoides*, *C. disticha* and *C. chordorrhiza* appear to be the favorite suscepts of *S. duriaeana* in Europe, *C. hudsonii* and its North American counterpart, *C. stricta*, appear to be the most common suscepts for *S. sulcata* in North America.

SCLEROTINIA LONGISCLEROTIALIS

PLATE V

As far as I am aware, *Sclerotinia longisclerotialis* Whet. has been recorded only from North America. I kept a sharp lookout for it wherever I collected in swamps and wet marshes in western Europe during 1930, but no specimens were found which might on any grounds be referred to this species. No *Sclerotinia* species was taken there on any of the *Carex* species on which *S. longisclerotialis* is known to occur. It seems therefore probable that it is a species restricted to North America.

Although this species is described, illustrated, and discussed in full in my 1929 paper (Whetzel 1929: 24–30, *fig. 10–13, 20–23*) a brief description is here presented for the convenience of the reader. A complete list of the species on which it is known to occur, including a new suscept made subsequent to those already listed (Whetzel 1929: 30), is recorded below.

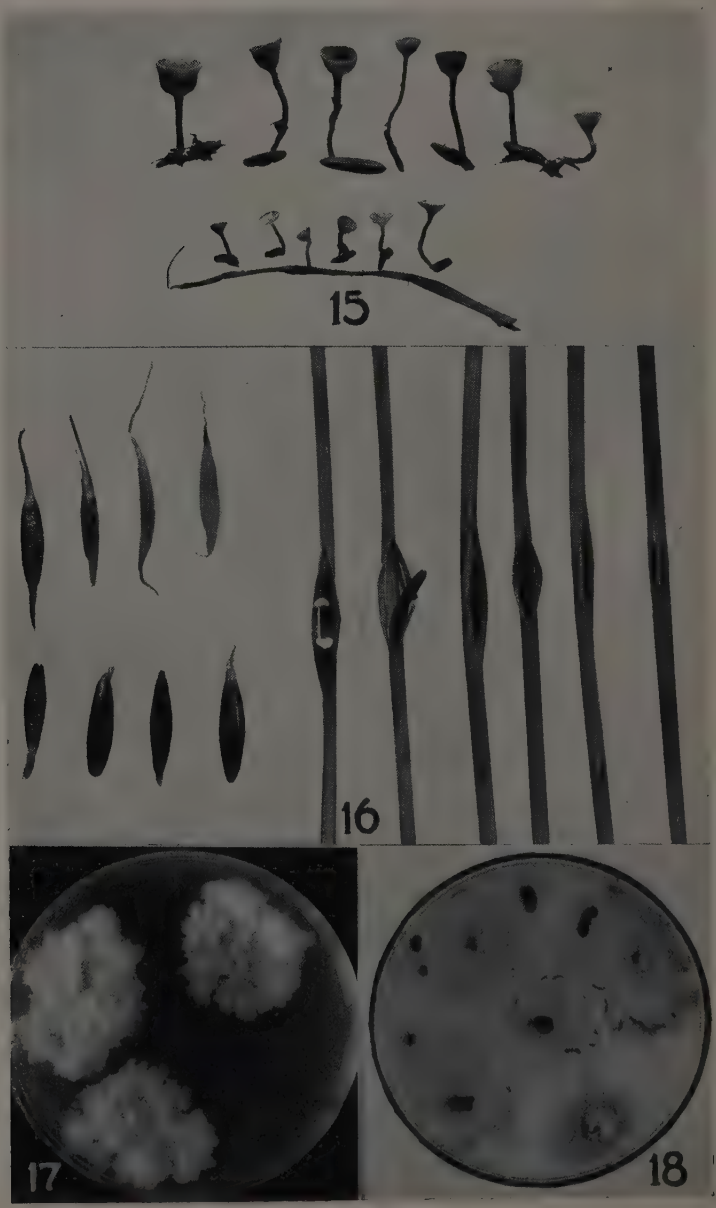

PLATE IV

SCLEROTINIA LONGISCLEROTIALIS Whetzel, Mycologia **21**: 24–30. 1929.

Spermodochidial groups (Figs. 20, 21) ovate, oblong, shining black, in pairs at rather regular intervals along two faces of the culm just below the inflorescence, rarely toward the base below the sclerotium, formed within the cortical tissues of the culm, exposed by slits in the epidermis through which ooze the mucilaginous masses of spermatia; *spermatia* globose 1–2 μ in diam., hyaline, produced in succession from the tips of obclavate spermatophores. External appearance and internal structure essentially as in *S. duriaeana* (see Whetzel 1929: *fig. 23*).

Sclerotia (Figs. 19, 22) usually one, sometimes two or more, in culm, remaining enclosed or slightly exposed by a slit in the epidermis (Fig. 20), never freed as are the sclerotia in *S. sulcata* or *S. duriaeana*, at maturity truncate, uniform in thickness, more or less 3-angled, striate due to pressure of the vascular bundles of the culm during development, at first cottony, becoming pinkish, then smoke gray, finally dull black without, the medulla white; variable in length and diameter according to the size of the infected culm, 1 cm. long by 1 mm. thick in *C. interior*, 7 cm. long by 2 mm. thick in *C. retrorsa* and 3 to 10 cm. long in *C. prairea*.

Apothecia (Fig. 19) thistle-, funnel-, or goblet-shaped with long slender stipe, one, rarely two or more, from each sclerotium; *cup* dark fawn-colored, smooth without, membranous, mouth constricted, never opening widely, 2–5 mm. broad; *stipe* slender, 10–50 mm. long, pale and smooth above, dark tomentose below; *asci* long, cylindrical, attenuate below the middle, 136 meas. from 5 apothecia from *C. prairea* gave 170–230 x 8.8–14.3 μ, mode 194 x 10.4 μ, av. 182.1 x 10.7 μ; *ascospores* strongly inequilateral, flat or incurved on one side, 289 meas. from 5 apothecia from *C. prairea* gave 12.6–22.8 x 5.3–12.5 μ, av. 18.3 x 8.1 μ, mode 21 x 9 μ; *paraphyses* slender, slightly clavate, septate.

In culture on potato dextrose agar forming an appressed feathery growth of aerial mycelium (Whetzel 1929: *fig. 20*) with distinct minute hard spermodochial masses. No sclerotia formed.

HABITAT: Open swamps and marshes where water stands throughout the year.

TYPE LOCALITY: Swamp south of the Lloyd Preserve, McLean, N. Y.

DISTRIBUTION: U. S. A.: New York and Maine; Canada: Lake Temagami, Ontario.

TYPE SPECIMEN: CUPP *10544* on *Carex prairea* Dewey, May 16, 1918. *Whetzel.*

MATERIAL EXAMINED: In addition to the specimens listed in 1929 (p. 30) on *Carex prairea* Dewey, *C. interior* Bailey, *C. vesicaria* L., *C. retrorsa* Schw., and *C. crinita* Lam. may be reported: On **C. prairea:** CUPP *17499*, McLean, N. Y. May 27, 1929 (apo-

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Plate 4. *Sclerotinia sulcata.* **Fig. 15.** Apothecia from culms of *C. stricta*; natural size. CUPP *11515*. **Fig. 16.** Sclerotia from culms of *C. stricta*; natural size. CUPP *14747*. **Figs. 17–18.** Cultures from *C. stricta* on potato dextrose agar showing cottony aerial mycelium, and sclerotia with spermodochidial masses respectively; ½ natural size. CUPP *11515* and *14747*.

PLATE V

thecia); — CUPP *23536*, McLean, N. Y. May 14, 1934 (apothecia). On **Carex oligosperma** Michx.: CUPP *17783*, Sand Point, and CUPP *17784*, near Bear Island, Lake Temagami, Ontario, Canada, both on September 16, 1929, *H. H. Whetzel & Geo. Thompson* (spermodochidia and sclerotia).

This species is doubtless common and widely distributed in northern United States and Canada. Localities where it occurs are readily discovered by looking during late summer for the dead and bleached culms with their characteristic spermodochidia and sclerotia.

Carex oligosperma Michx. is here for the first time recorded as a suscept of *S. longisclerotialis*.

SCLEROTINIA CARICIS-AMPULLACEAE

PLATE VI

Of all the species of *Sclerotinia* known to me on sedges and rushes, *S. caricis-ampullaceae* Nyberg is the largest, the most striking, and to the eye of a mycologist, the most beautiful. This species was first brought to my attention by Dr. John Nannfeldt of the University of Upsala. He sent me in February, 1933 a collection taken June 25, 1932 near Lake Gärdsjön in Sweden. I recognized it at once as an undescribed species and proposed to Dr. Nannfeldt that I publish a description of it, naming it in his honor. Fortunately I delayed the preparation of the manuscript. A year later, in February 1934, I received another specimen of this species from Dr. Nannfeldt which had been collected in Finland. Along with the specimen he sent me a preliminary description of the species prepared by the collector, Mr. Wolmar Nyberg, who was publishing it under the name the species now bears. Nyberg, amateur mycologist and banker, had discovered it in early June 1930, in a sphagnum bog on his villa grounds near Vessö in the parish of Borgä, where it appeared each succeeding spring. Nyberg's description of which he sent me a reprint appeared in the Finnish scientific journal cited below.

During the winter of 1937–38, Dr. W. G. Solheim of the University of Wyoming told me of a remarkably large and beautiful species of *Sclerotinia* on *Carex aquatilis* which his colleague, Dr. C. L. Porter, had discovered in a high mountain swamp in the Medicine Bow Mountains, in June 1937 (Fig. 25). Duplicate specimens of Porter's collection together with abundant collections made by Solheim in 1939 and in succeeding years proved it to be conspecific with the Scandinavian collections. The extraordinary size and unusual form of the sclerotia of *S. caricis-ampullaceae* distinguish it at once from the other species on *Carex*. Although known from but three localities, its occurrence in Scandinavia and the high mountains of Wy-

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Plate 5. *Sclerotinia longisclerotialis*. **Fig. 19.** Apothecia attached to the sclerotia, from culms of *C. prairea*; natural size. CUPP *23536*. **Fig. 20.** Spermodochidia and enclosed sclerotia, from culms of *C. interior*; natural size. CUPP *15868*. **Fig. 21.** Spermodochidia, x6, from culms of *C. vesicaria*. CUPP *15860*. **Fig. 22.** Young sclerotia exposed by cutting away the culm epidermis, x2, in culms of *C. prairea*. CUPP *15872*.

PLATE VI

oming suggests that it is probably common wherever its suscepts occur throughout the sub-arctic isothermal zone.

An extensive treatment of this species is to be found in the paper by myself and Solheim (1943).

SCLEROTINIA CARICIS-AMPULLACEAE Nyberg, Mem. Soc. pro Fauna et Flora Fenn. **10:** 20–23. 1934.

Spermodochidial groups (Fig. 24) when fresh, dark colored, tuberculate, more or less spaced at intervals along the culm just below the inflorescence, exposed by slits on two faces of the culm; *spermatia* hyaline, globose to slightly ovate, 2.5–3 μ in diam., produced successively from the tips of clustered obclavate spermatophores, oozing forth in mucilaginous drops.

Sclerotia (Fig. 24) extraordinarily large, variable in size up to 20 cm. long by 1 cm. thick near the base, ventricose below with rounded or bluntly attenuated base, gradually elongated above into a slender whip-like apex, developed within the slender 3-angled culm, the base firmly nestled in the very base of the culm and the enclosing leaf bases, breaking forth through a slit in the epidermis of the culm to expose the lower half or so, the slender pointed tip remaining firmly enclosed, black without, sulcate, within pale pink to white, firm.

Apothecia (Figs. 23, 25) usually several to many, fasciculate, arising at one point on the exposed surface of the sclerotium, long-stipitate; *cup* thistle-funnel-shaped becoming more or less expanded, vinaceous brown, 4–22 mm. in diam. by 7–16 mm. deep, outside finely tomentose, relatively thin (1 mm.), membranous; *stipe* long, slender, flexuous, varying in length depending upon the depth to which the sclerotium is immersed, only the cup and upper part of the stipe protruding from the water or moss; *asci* cylindrical, attenuated below, apex rounded and thickened, pore faintly J+, 192–213 x 11.8–13.5 μ, 8-spored, spores uniseriate; *ascospores* ellipsoid, hyaline, smooth, without oil drops, 13.5–16.9 x 8.5–10 μ; *paraphyses* filiform, hyaline, branched below, scarcely enlarged toward the tips, 1–2 μ in diam.

HABITAT: In culms of *Carex aquatilis* Wahl., *C. aquatilis* Wahl, var. *altior* (Rydb.) Fern., and *C. inflata* Huds. in wet swamps and mossy bogs in sub-arctic or high mountain regions.

TYPE SPECIMEN: On *Carex inflata* Huds. (= *C. ampullacea* Good.), sphagnum bog near Vessö, parish of Borgä, Finland, June 19, 1931. Coll. W. Nyberg. Part of type deposited in CUPP *28912*. Dupl. in Bot. Inst. Univ. Upsala, Sweden.

DISTRIBUTION: Finland, Sweden, and Wyoming, U.S.A. Apothecia June–July, spermodochidia and sclerotia late summer and autumn.

Plate 6. *Sclerotinia caricis-ampullaceae*. **Fig. 23.** Apothecia from sclerotia in culms of *C. aquatilis* var. *altior* (specimen from preserving solution). CUPP *28910*. **Fig. 24.** Spermodochidia and sclerotia in culms of *C. aquatilis* var. *altior*; natural size. CUPP *29268*. **Fig. 25.** Apothecia in their natural habitat; natural size.

MATERIAL EXAMINED: In addition to the type material, I have had in hand: On **Carex aquatilis** Wahl.: —Collection made at Selet, near Lake Gärdjön, prov. Västerbotton, parish of Lövänger, Sweden, June 25, 1932, *G. Lohammar*, CUPP *21965*, (dupl. in Herb. Bot. Inst. Univ. Upsala). On **Carex aquatilis** Wahl. var. **altior** (Rydb.) Fern.: numerous collections (Whetzel & Solheim 1943: 397) made below Nash Fork bridge near Univ. Wyoming Science Camp in the Medicine Bow Mts. (alt. 9,600 ft.), Albany Co., Wyo. during the years 1937, 1939, 1940, 1941, and 1942, *W. G. Solheim & C. L. Porter*. On **Carex inflata** Huds., *Solheim*, same locality, June 27, 1942. Duplicates of all these collections are deposited in the herbarium of the University of Wyoming and the Plant Pathology Herbarium, Cornell University. The collection of apothecia made June 26, 1939 on *C. aquatilis* var. *altior* has been distributed by Solheim as *204*, Mycoflora Saximontanensis Exsiccata.

SPECIES ON ERIOPHORUM

As far as I have been able to find, there is but one species of *Sclerotinia* reported on *Eriophorum*. This is *Sclerotinia vahliana* described by Rostrup (1891: 607) from specimens collected by J. Vahl, S. Hansen and N. Harz on botanical expeditions at various times on the west coast of Greenland. The earliest collected specimen which Rostrup had before him when he described this species is presumably one collected by J. Vahl for whom he named the species. A specimen preserved in the Rostrup collections in the University Botanical Museum, Copenhagen, bears the label "E. Rostrup's Svampesamling. 1. Sclerotinia Duriaeana Tul. (Carex rigida). Nonnese 5/1829 by J. Vahl." Through the kindness of the director of the museum, Johs. Grøntved, this specimen was loaned me in September 1927 (Fig. 28). A critical examination satisfied me that this is not *S. duriaeana* and that the suscept is a species of *Eriophorum*. Whether or not this is one of the specimens on which Rostrup based his description it is now impossible to say. Since this is earliest known collection of the species and was collected by J. Vahl, I am designating it the type specimen of *S. vahliana* Rostr.

SCLEROTINIA VAHLIANA

PLATE VII AND TEXT FIG. B

Rostrup gives *Eriophorum scheuchzeri* as the suscept for all the collections he had from Greenland and lists, in addition to Vahl, two other collectors, S. Hansen and N. Harz, who appear to have made their collections during the years 1888 and 1889 (Rostrup 1891: 593). These specimens were presumably deposited in Rostrup's collections in the Botanical Museum in Copenhagen, but I have no record of having seen them when I was there in 1930.

I know of but two other collections identified as *S. vahliana*. One of these is a collection made by J. A. Nannfeldt in northern Sweden in 1927 on *Eriophorum angustifolium* and another collected by Vestergren, *et al.* in the same region in 1903 on the same species and distributed under *730*, in Vestergren's Micromycetes Rariores Selecti. These agree well in all their characters with the type collection.

During the summer of 1930 I made collections of a *Sclerotinia* attacking *E. angustifolium* (Fig. 26) in Denmark and in southern Sweden. I was able

to study only the early stages of the infection which was developing while I was there during the months of June and July. I obtained the fungus in pure culture (Fig. 27) and also found the sclerotia in early stages of development in culms in the field. Such evidence as I was able to get, indicates that the fungus in these collections is probably *S. vahliana*.

It seems desirable to present here a translation of Rostrup's original description.

"376. *Sclerotinia Vahliana* n. sp.

"Apothecia arising from a sclerotium, stipitate, brown or castaneous. Cup hemisphaerical, length and height, 4–8 mm. Stipes flexuous, tomentose, striate below, 1–3 cm. long, about 1 mm. thick. Asci cylindrical-clavate, long stipitate, length (including stipe) 150–170 μ x 8–10 μ. Spores ellipsoid, 11–14 x 4–6 μ. Paraphyses numerous. Sclerotia black, oblong, compressed, sulcate, 1 cm. long by 0.5 cm. thick.

"Between the leaf sheaths of *Eriophorum Scheuchzeri* Hoppe, Greenland (Vahl), Umanak (S. Hansen), Egedesminde, Holstenborg, Godthaab (N. Harz).

"Sclerotia assembled, 2–3, between the lower leaf sheaths, with 3–4, deep furrows along the outward turned, free side."

Based upon Rostrup's original description of the apothecia and my studies on the specimens above referred to, the following would appear to be a fairly complete description of this species.

SCLEROTINIA VAHLIANA Rostr. *In* Tillaeg til "Grønlands Svampe (1888)." Meddel. om Grønland. **3:** 607–608. 1891.

Spermodochidia not found.

Sclerotia (Fig. 28 and Text Fig. B) variable in size and shape, shell-like in the form of a short, lobed half-cylinder or hollow hemisphere, up to 2–3 cm. in circumference, about 2–3 mm. thick, black without, white within, surface rough, irregularly and deeply creased, with low ridges, usually 3–4 in each culm, obviously originating within the culm but finally breaking forth to complete its growth. This peculiar morphology of the sclerotia has been recorded by Rostrup (1903: 315) who quotes a note by Ostenfeld, the collector of specimens of this species from Iceland: "Sklerotierne höjst uregemaessigt bugtet-foldede" (Sclerotia very irregularly curved and creased). The internal structure is essentially like that of other species of *Sclerotinia*.

Apothecia (Figs. 29, 30) 1–several arising fasciculately from some point on the sclerotium, broadly and deeply cup-shaped, castanean brown, short stipitate; *cup* up to 10 mm. broad by nearly as deep; *stipe* 1–3 cm. long x 1 cm. thick, flexuous, tomentose, darker than cup, black toward base; *asci* cylindrical clavate, long-attenuate below, tip rounded, not thickened, 50 meas. (type) 109–164 x 7.8–10.4 μ, mode 151.7 x 9 μ, av. 144 x 8.6 μ, 8-spored, spores uniseriate; *ascospores* long ellipsoid to fusoid, flat to concave on one side, biguttulate, 50 meas. (type) 10.8–18 x 4.8–6.6 μ, mode 12 x 5.4 μ, av. 13 x 5.6 μ; paraphyses numerous, slender, simple or branched, 3 μ diam., slightly or not at all enlarged at the tips.

In culture (Fig. 27) on potato dextrose agar forming a sparse white webby aerial mycelium; submerged mycelial mat dark olivaceous brown.

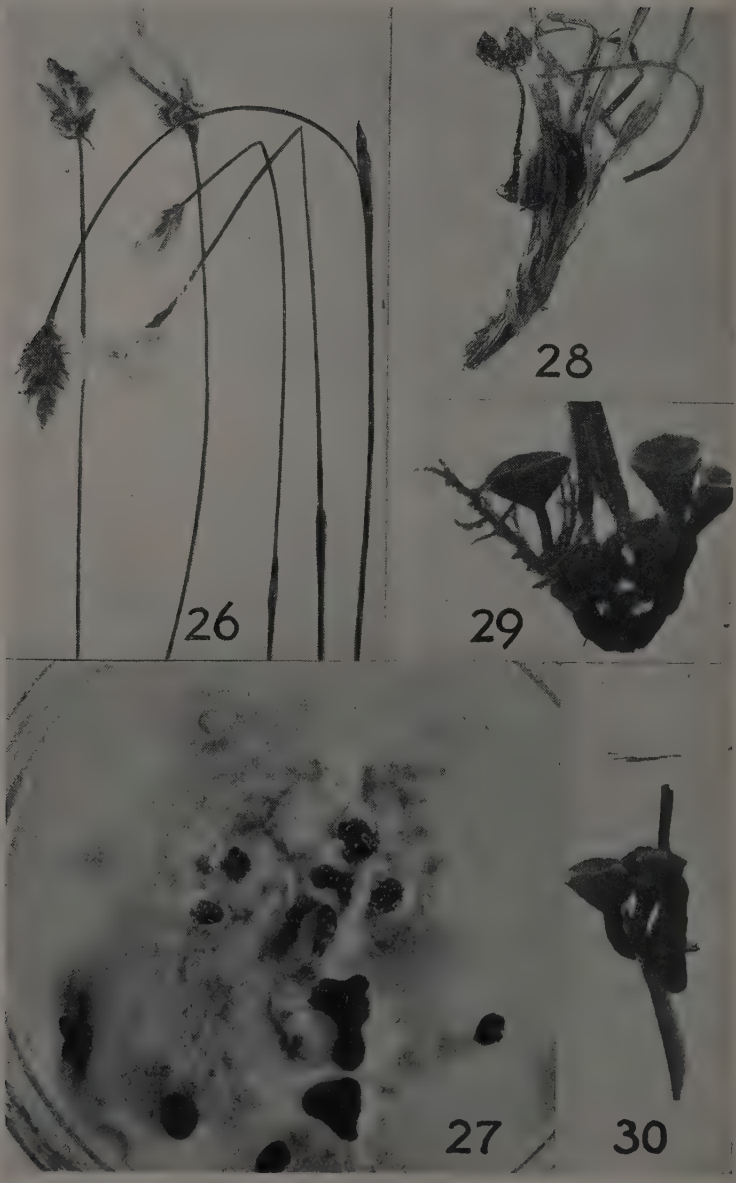

PLATE VII

Sclerotia formed abundantly, irregularly discoid or oblong, flat or low loaf-shaped (from diseased stems collected near Lyngby, Denmark).

HABITAT: In the culms of *Eriophorum scheuchzeri* Hoppe, *E. vaginatum* L., and *E. angustifolium* Roth. in sphagnum bogs, apothecia, May–July; sclerotia, late summer and autumn. An arctic and sub-arctic species.

DISTRIBUTION: Reported from Greenland (Rostrup 1891 and 1906), and Iceland (Rostrup 1903 and Larsen 1932). Known to me from Denmark and Sweden. Should be found in the arctic and sub-arctic zones of continental North America.

TYPE SPECIMEN (Fig. 28): The collection by J. Vahl on *Eriophorum* (*scheuchzeri* ?) Nonnese, Greenland, May 1829. Deposited in the Botanical Museum, Copenhagen, under the name, "*Sclerotinia Duriaeana* Tul." Photograph and microscopic mount deposited in CUPP *16275*.

MATERIAL EXAMINED (in addition to the type specimen): On **Eriophorum vaginatum** L.: CUPP *31589*, sphagnum bog along north shore of Lyngby Sö, Lyngby, Denmark, June 7, 1930, *H. H. Whetzel* (early stages of infection); — CUPP *31591*, swamp in forest at Nosten, parish of Bondhyrho, near Upsala, Sweden, July 3, 1930, *H. H. Whetzel & J. A. Nannfeldt* (early stages of infection). On **Eriophorum angustifolium** Roth. (=*E. polystachon* L.): Vestergren, Micromycetes Rariores Selecti, *730*. Lapponica Tornensis, Vassijaure (Sweden), July 1903, *A. Roman, N. Sylvén & T. Vestergren* (apothecia and sclerotia); — "Fungi Suecici". University Upsala. Dupl. N. Y. Bot. Gard. and CUPP *31606*. Collected in Torne, Lappm. Jukkasjarvi. s:n. Abisko, Sweden, June 30–July 5, 1927, *J. A. Nannfeldt* (apothecia and sclerotia); — CUPP *31590*, swamp in forest near Nosten, parish of Bondhyrho, near Upsala, Sweden, July 3, 1930, *H. H. Whetzel & J. A. Nannfeldt* (early stages of infection).

This species is very distinct from the others in cyperaceous suscepts, being especially marked by the unusual form and development of its sclerotia. While I think that the *Sclerotinia* which I found in its early infection activities in the culms of *E. vaginatum* and *E. angustifolium* in Denmark and Sweden is probably *S. vahliana*, it is unfortunate that I was not early enough in the localities to get the apothecia and did not remain late enough in the summer to follow the development to mature sclerotia. I feel quite sure that spermodochidia of some type would have developed during late July or August in the infected culms. Tiny masses of densely protoplasmic, large, thin-walled hyphae, which are present at intervals in the diseased culms which I preserved (CUPP *31589*) are characteristic of the initial stages of spermodochidial development in the other species of the cypericolous species of *Sclerotinia*.

The sclerotia of *S. vahliana* appear to have an unusual history of development (see Text Fig. B). They are initiated as in the related species, within the culms of the suscepts. I was able to observe only the early stages in

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Plate 7. *Sclerotinia vahliana*. **Fig. 26.** Diseased culms of *Eriophorum vaginatum*; ½ natural size. CUPP *31589*. **Fig. 27.** Culture from culms of *E. vaginatum* on potato dextrose agar showing sclerotial formation; natural size. CUPP *31589*. **Fig. 28.** Type specimen in Botanical Museum, Copenhagen (revived dry material); natural size. CUPP *16275*. **Figs. 29–30.** Apothecia on sclerotia from *E. angustifolium* from Sweden (revived from liquid preservative); natural size. CUPP *31606*.

this development. The sclerotia begin as elongate, cottony, white masses at three or four places in the culm. As the young sclerotia begin to solidify they become pink in color as do those of related species. In a few cases I found evidences of the developing rind. I found no mature sclerotia, all being still firmly enclosed within the culms. I observed that the infected culms often appeared to be stouter and apparently to have been more vigorous in their growth than were the healthy ones. This may have been due to stimulation by the fungus during the first days of infection. As far as I was able to discover, these sclerotia were developing only in the upper internode of the culm in *E. vaginatum*. It seems almost certain, however, that sclerotia are formed at intervals throughout the culms even to the base. They apparently do not complete their development within the culm but,

TEXT FIG. B

Text Fig. B. Sclerotium of *Sclerotinia vahliana* from base of culm in crown of *Eriophorum*, (a) front and (b) back view, (c) from one higher up in culm; all x2. Drawn by Miss Charlotte Dill.

bursting out, continue to grow in size. The mature sclerotia I have seen bearing apothecia are obviously too large to have fully matured within the culms.

Rostrup's description of the sclerotia as "assembled between the lower leaf sheaths" suggests that in the dwarfed *Eriophorum* plants of Greenland and Iceland, they may be formed chiefly in the basal region of the culm. However, I have seen specimens of sclerotia bearing apothecia which had clearly developed in the upper reaches of the culm (*e.g.* Nannfeldt's collection of 1927, Text Fig. Bc). Careful observations in the field may disclose, in the case of sclerotia clustered in the crowns of the suscepts, that the base of the leaves as well as the culm have been involved in the nourishment of these sclerotia. Larsen (1932), in recording the occurrence of this species in Iceland, cites collections by himself and by Ostenfeld and remarks, "On tufts of Carex and Eriophorum on swampy ground. The pea-sized sclerotia are often seated in the axils of the leaves, covered by the leaf sheaths". It is very doubtful that *S. vahliana* ever attacks *Carex* species. Larsen is either

in error or has confused some species of *Sclerotinia* actually occurring on *Carex* in Iceland, with *S. vahliana* on *Eriophorum*.

SPECIES ON SCIRPUS AND SCHOENUS

A species of *Sclerotinia* on *Scirpus lacustris* L., long known to European mycologists, chiefly in its sclerotial stage, was finally described by Rehm (1896) under the name of *Sclerotinia scirpicola*. Although represented in herbaria by but few collections, it is certainly common and widely distributed throughout northwestern Europe. It is not known from North America. No species of *Sclerotinia* is known to occur on other species of *Scirpus*. Ferdinandsen & Winge (1911: 293) report a collection by Ade in Bavaria, Germany, said to be this species on *Scirpus silvaticus* ("the spores finally becoming 2-celled"). Since the spores of *S. scirpicola* are uniformly 1-celled, it is very doubtful that Ade's specimen was correctly determined. There is however a species, pathogenic to the closely related *Schoenus nigricans* L., which appears to have been generally overlooked by mycologists.

SCLEROTINIA SCIRPICOLA

PLATE VIII AND TEXT FIG. C

This species is of peculiar interest because of the nice adaptation it has made to its aquatic habitat. Its suscept is an inhabitant of the shallow waters of lakes and ponds. Not only do the freed sclerotia float like tiny corks upon the water but in the spring the apothecia develop on these where they accumulate in thousands on the low flat shores as the water subsides. Aside from the original description of the apothecial stage by Rehm (based upon dry material) the papers by Ferdinandsen & Winge (1911 and 1913) and Sydow's (1912) appear to be the only contributions of importance dealing with this species. During my stay at Lyngby, Denmark, during June 1930, an exceptional opportunity was afforded for study of *S. scirpicola* as it occurs in Lyngby Sö. As a result of these studies a more complete picture of this species can now be drawn.

SCLEROTINIA SCIRPICOLA Rehm *in* Rabenh. Krypt. Fl. 1^3: 822. 1893.

Sclerotium roseum Moug. *in* Fries, Syst. Myc. **2** (Suppl.): 43, 1830. (=Elench. Fung. **3:** 43. 1828).

Sclerotium roseum Kneiff *in* Duby, Bot. Gall. **2:** 874. 1830.

Sphacelia scirpicola Ferd. & Winge, Biolog. Arbej. Tilegnede, Warming, Nov. 3, p. 290. 1911.

Myrioconium scirpi Syd. Ann. Myc. **10:** 449. 1912.

Myrioconium scirpicola V. Höhn. Mitt. Bot. Inst. u. Tech. Hochsch. Wien **3:** 50. 1926.[6]

Spermodochidial groups (Figs. 31, 32) more or less oval to elongate, shallow, slightly raised, very variable in size, often minute, irregularly

[6] Ferdinandsen & Winge (1913: 24) admitted the logic of Sydow's argument (in a letter) for referring the conidial stage of *S. scirpicola* to his genus *Myrioconium* but they did not actually make the combination *M. scirpicola*, as Von Höhnel seems to imply in this 1926 paper.

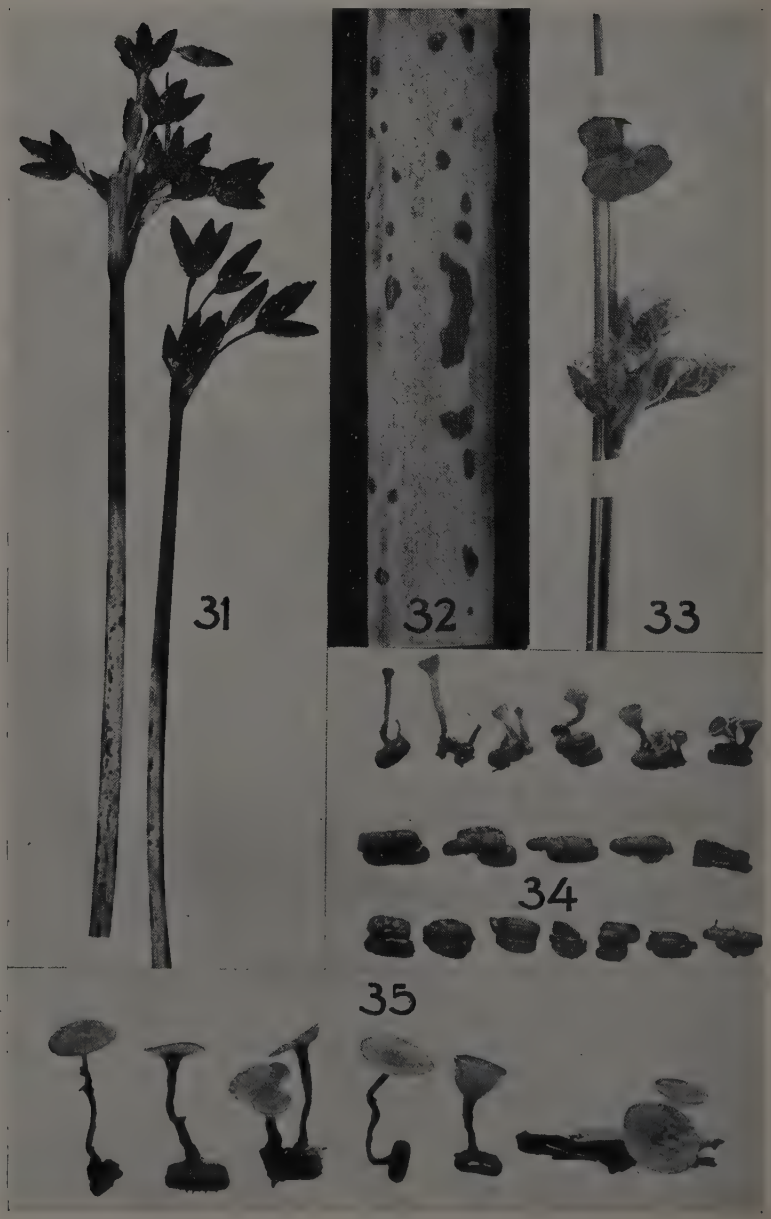

PLATE VIII

disposed along one side of the culm for some distance just below the heads, dull black, rupturing by slits in the epidermis, from which the viscid mass of spermatia are discharged; *spermatia* minute, globose, about 3.3 μ in diam. The dark color of the spermodochidial groups is due to the brownish color of the massed spermodochia, the brown gummose contents of the epidermal cells, and to brown-walled intercellular hyphae in some of these cells.

Sclerotia (Fig. 34) usually 8–10 per culm, the first one developing with the appearance of the spermodochidia and just below them; successive sclerotia appear a few inches apart as the invading hyphae spread downwards in the culm. The sclerotia originate as soft pinkish mycelial masses in the loose central parenchyma of the culm, at maturity appearing as large, longitudinally lobate, oblong, blunt, black, tuberoid bodies completely enclosed in the culm. The culms, weakened at these points, are easily broken by the wind, discharging the sclerotia into the water, where they float, and drifting with the wind, accumulate, together with broken pieces of the culms, in great patches along the leeward shores of the lake or pond. The sclerotia vary much in shape and size, being usually somewhat longer than broad, ranging from 2–10 mm. by 2–5 mm. in diameter. The form of the sclerotium is striking, being elongately 2–3-lobed, the ends of the lobes blunt and rounded. This compound appearance is more apparent than real, being due to the structure of the culm. A cross section of the sclerotium discloses a narrow outer black rind, one to two cells thick, enclosing a medulla of rather loosely interwoven, relatively thin-walled, large hyphae, distinctly septate and often constricted at the septa. The medulla long retains its bright pink color, even after the formation of the rind, but eventually becomes white. The lobation of the sclerotium is marked out in the cross sections by faint brown lines, the persistent brownish-walled cells which formed the firmer tissues surrounding the cavities originally filled with thin-walled pith cells which have been largely digested by the developing sclerotium.

Apothecia (Figs. 34, 35) appearing in the spring at flowering time of the *Scirpus*; 1–to several from each sclerotium, usually not more than 2, arising at any point on the sclerotium, variable in size, when fully expanded 3–15 mm. in diam., av. 8–10 mm. The size of the apothecium apparently does not depend entirely upon the size of the sclerotium for several, all usually small, or one much larger than the others may arise from a single sclerotium; *cups* deep goblet-shaped becoming nearly flat expanded, light fawn to vinaceous brown, lighter beneath, due to a coating of fine hyphal fuzz; *stipe* usually short, slender, concolorous with under side of the cup, also covered with a hyphal fuzz above, clothed below, especially at the base, with a dense mat of long, dark hyphae which serve to anchor the large apothecia to the

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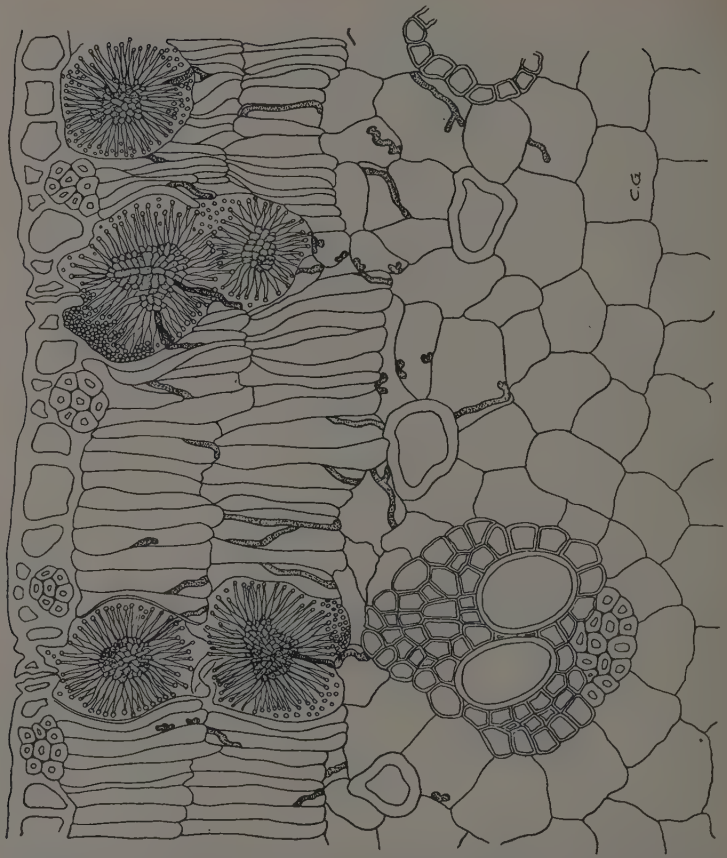
Plate 8. *Sclerotinia scirpicola.* **Fig. 31.** Diseased culms and inflorescence of *Scirpus lacustris* showing spermodochidia; about natural size. **Fig. 32.** Part of culm showing spermodochidia, x6. **Fig. 33.** Showing method of inoculating pistils of *S. lacustris* for study of invasion phenomena; about natural size. **Fig. 34.** Sclerotia and young apothecia; natural size. **Fig. 35.** Sclerotia bearing mature apothecia; natural size. All from specimens in CUPP *31607*.



Text Fig. C. Cross section through spermodochidia of *Sclerotinia scirpicola* about x400. Note that each cavity is directly beneath a stomate, and is formed chiefly by crowding aside the palisade cells rather than by digesting them. Drawn by Carlos Garcés.

surrounding floating debris of broken culms; *asci* long, cylindrical, apex blunt, of about the same diameter throughout, except at the base where they are rather sharply narrowed to about half the diameter of the apical portion, 8-spored, spores uniseriate in the upper third of the ascus, 50 meas. (fresh, in water) 133.3–181.8 x 8.1–10.8 μ, mode 157.5 x 9.5 μ, av. 153.2 x 9.4 μ; *ascospores* long oval, 100 meas. (fresh, in water) 11.2–17.8 x 5.3–7.9 μ, mode 13.8 x 6.6 μ, av. 14.4 x 6.6 μ surrounded by a very evident mucilaginous coat; on germination in water often producing spermatophores and spermatia directly; *paraphyses* slender, not appreciably swollen toward the tips, about 3.4 μ in diam.

In culture on potato dextrose agar forming a thin, white, aerial, webby coating over the surface of the agar; submerged mycelium feathery as in cultures of *S. longisclerotialis*; no sclerotia formed.

HABITAT: In the culms of *Scirpus lacustris* L. in the shallow waters of lakes and ponds. Apothecia developing on sclerotia stranded along the shore line among sedges, grasses and other plants which afford continuous shade and moisture during their development.

DISTRIBUTION: Throughout western Europe; very abundant in Denmark (Ferdinandsen & Winge 1911: 293). Also reported from Finland, Germany, Sweden, and England. Probably to be found in equal abundance when sought in neighboring regions of northern Europe; not known from North America.

TYPE SPECIMEN: The specimen upon which Rehm (1893: 823) based his original description of this species, was found by him in Winter's herbarium. He says it bore the label "Peziza tuberosa" with the notation (transl.) "in May, the old culms of *Scirpus lacustris*, in our lakes break up. When these fall into the water, this Peziza appears from sclerotia in a few days, from every piece which with us very frequently contains *Sclerotium roseum* (Moug.) Fries." According to Rehm the specimen was probably collected by Winter in Saxony near Zweibrücken in the Rheinpfalz (Germany). I have been unable to discover where this type specimen (if indeed it is still extant) is now deposited.

ILLUSTRATIONS: Ferdinandsen & Winge, Saertryk af Biol. Arbej. Tilegnede. Eug. Warming. Nov. 3, *fig. 1–7*. 1911.

MATERIAL EXAMINED: Exsiccati Specimens: In the Kew Herbarium there is a specimen of three pieces of culm each with an enclosed sclerotium labeled "Sclerotium roseum" with a brief written description signed by Persoon. The specimen is unnumbered, undated and locality where collected not indicated; — Mougeot et Nestler, Stirp. Crypt. Vogeso-Rhen. *884* (1826). "*Sclerotium roseum* Kneiff-Pers.-Fries. in Litt." Specimens of this in the British Museum, in Kew, and at Cornell show sclerotia in culms said to have been collected near "Argenoratum", now Strassburg, in Alsace, France. Collected by Kneiff in autumn. No date of collection given; — Kneiff et Hartmann; Pl. Crypt. Badens, *20*, 1828. "Sclerotium roseum Kneiff (nov. sp.)". This specimen in the British Museum consists of pieces of culms containing mature sclerotia collected in canals along the Rhine near Kehl in Germany. Sept.–Oct. No year of collection given and no collector cited; — Klotzsch, Herb. Mycol. *244* (1842). "Sclerotium roseum Moug. Intra culmos Scirpi lacustris ad Dresden". This specimen in Kew Herbarium bears only the data above quoted. It consists of a piece of culm containing a sclerotium; — Roumeguère, Fung. Gallici Exs. *499*, 1879. "Sclerotium roseum Kneiff. Pers. Fries. in Litt. Moug." This number was made up from material remaining in Mougeot's herbarium and is of the same origin as his Stirp. Crypt. Vogeso-Rhen. *884*. Specimens examined in the Kew Herbarium and in CUPP show a single sclerotium in a piece of culm; — Otto Jaap, Fung. Sel. Exs. *755*. Collected by Jaap in Brandenburg, Triglitz in the Prignitz, Germany. June 15, 1916 (spermodochidia (?), sclerotia and apothecia); — Flora Suecici *4222*. Collected by J. A. Nannfeldt on shore of shallow arm of Mälaren. Bondkyrok s:n. Skarholmen, Uppland, Sweden. June 25, 1931 (apothecia). Dupl. CUPP *32615*; — In Kew Herbarium a specimen labeled: "*Sclerotinia scirpico'a*, Ashgrove Loch, Shevenston, Ayrshire 26.2.21. Coll. D. A. Boyd." Consists of a single culm of *S. lacustris* containing a single sclerotium; — CUPP *31607*, along the shore of Lyngby Sö, Lyngby, Denmark, June 3–July 13, 1930, *H. H. Whetzel* (spermodochidia, sclerotia, apothecia and cultures). Duplicate specimens from this collection have been distributed

to the following herbaria: Kew, England; British Mus., London; Univ. Toronto, Canada; Farlow Herb., Cambridge, Mass.; N. Y. Bot. Gard.; Univ. Mus., Ann Arbor, Mich.; Missouri Bot. Gard., St. Louis, Mo.; Mycol. & Pl. Dis. Survey, Bur. Pl. Ind., Washington, D. C.; Univ. California, Berkeley; Univ. Iowa, Iowa City.

The abundance of apothecia in Lyngby Sö during my stay in Lyngby, and the nearness of laboratory facilities for critical studies and culture work, presented an opportunity not to be neglected. I devoted most of my time to such studies, the results of which are summarized below.

LIFE HISTORY STUDIES

The life history of *S. scirpicola*, while in general quite like that of its near relatives on *Carex* species, presents some unique features largely due to the habits of its suscept *Scirpus lacustris*. This *Scirpus* grows in the shallow waters along the shores of the lake. It is most vigorous and fruits most luxuriantly near the shore, the plants becoming more scattered, shorter and usually producing fewer flowering culms as the plantation spreads out into the deeper water. When we arrived at Lyngby, the first week in June 1930, I found the apothecia already developing in great abundance from the thousands of sclerotia lodged in debris on low-lying projections of the shore, a few minutes' walk from the laboratory of the Phytopathological Experiment Station in which we were kindly afforded working facilities by the Director, Mr. Ernest Gram. The shores of this shallow lake are fringed with great patches of *Scirpus lacustris* and the prevailing southwest winds of the previous fall and winter had deposited the sclerotia in immense numbers along with the broken culms of *Scirpus* just above the receded water level on every flat projection of the northeast shore of the lake and on the water where they were anchored and shaded by a rich growth of grasses and other shore-loving plants and shrubs. The open apothecia reached their maximum abundance about the end of the first week in June. A week later most of the apothecia were shrivelling or decaying, though new ones were still to be found just sprouting from sclerotia here and there. By the 17th of June, only an occasional apothecium was to be found. Many heads of the *Scirpus* were already in bloom on June 2 when we arrived, but blossoming reached its maximum about the time apothecia were to be found in greatest abundance. The weather throughout June was warm, the skies clear, and practically no rain fell. From the abundance of mature apothecia at the beginning of June, we judge that they must have begun to open about the middle of May. This would indicate that the period of apothecial production normally extends over a period of three to four weeks.

The mature apothecia discharge their ascospores in tiny puffs which, caught by gentle air currents among the shading vegetation, are wafted upward, some of them eventually reaching the white extruded pistils of the *Scirpus* inflorescence, where they lodge on the feathery stigmas. By suspending open apothecia over the inflorescence (Fig. 33) of culms (with cut ends in water) placed under an inverted large test tube, I was able to obtain naturally inoculated pistils. These when removed and mounted on glass slides the following morning, afforded excellent material for study of spore

germination and penetration. The spores germinate promptly, sending out from one end a stout simple germ tube. This penetrates the projecting hyaline cells of the stigma, usually forming a swollen globose appressorium where the tip has applied itself to the surface of the stigmatic cells. From this appressorium a penetration tube is sent into the cell from which an invasion hypha passes down into the tissues of the pistil. Infection is promptly indicated by the browning and shrivelling of the pistils. Uninoculated pistils remain white and plump for several days under the same conditions. The fungus having entered the ovary, growth seems to be greatly slowed down. In the open, about two weeks after inoculation, one or more of the peduncles supporting the individual spikes of the inflorescence begin to turn brown, the mycelium having killed the spike and spread downward into the peduncle through which it reaches the main stalk of the culm.

A dark browning just below the point of attachment of the inflorescence announces the invasion and infection of the culm proper. Visible infection of the culm becomes evident about three weeks after inoculation, as Ferdinandsen and Winge had already discovered. Rapid progress of the infection down the culm, however, does not usually occur for another week or so. It is evidenced by a hydrotic discoloration of the culm, with disappearance of the chlorophyll and discoloration in the form of alternating broad bands of a light and dark brown color. When this zonation has extended a foot or so down the culm, the spermodochidial groups begin to appear in an irregular line on one side of the culm in the brown necrotic tissues several inches below the inflorescence (Fig. 31). These spermodochidial areas are very variable in size, ranging from mere specks to elongate or irregularly ovate, black, slightly raised patches just beneath the epidermis. They are usually very numerous and the tissues in which they develop are generally of a distinctly lighter brown color than the adjacent regions. They finally rupture by slits, discharging the viscid masses of spermatia as the first sclerotial initials are to be detected just below. The downward progress of the fungus, indicated by hydrosis and zonate discoloration, now proceeds rapidly with the successive formation of sclerotial initials at intervals of a few inches. As many as ten to fifteen sclerotia may appear in a long vigorous culm, according to Ferdinandsen and Winge. When we left Lyngby on July 15, the first sclerotia were just beginning to appear occasionally in an infected culm.

As the sclerotia mature, they rupture the epidermis over them by several slits. The dead culms, weakened at these points, are gradually broken over by the winds of late summer and autumn. The breaking up of the ice in the spring by storms completes the breaking up of the culms, freeing the sclerotia which float on the surface of the water and are thus transported by the waves to their final resting place among the debris along the shore, ready to germinate and produce apothecia under the favorable conditions of temperature, shade, and moisture prevailing at the blossoming time of the *Scirpus*.

Ascospores discharged onto potato dextrose agar or disinfested segments of infected culm of *Scirpus* planted in the same medium give identical mycelial growths. Growth both from ascospore sowings and from tissue plantings is prompt and vigorous, like that of *S. sulcata*. Aerial mycelium is abundant, usually loose and cottony, at first pure white (never pink) becoming denser with age and faintly brownish, often with large dense masses of a dirty grey color, especially in test tube slants. The submerged mycelium becomes blue black at the center of the colony with radiating dark brown feathery strands. Spermodochia were not observed on this medium. Sclerotia were only tardily developed on test tube slants but were numerous in Petri dish cultures, being globose, black outside, pink where they grow against the glass and more or less completely buried in the dense aerial mycelium.

Although the morphology and life history of *S. scirpicola* are now perhaps more fully known than those of any of the related species on cyperaceous suscepts, a number of features require further consideration.

It seems probable that some of the sclerotia may remain dormant through the summer following their formation, as numerous hard, plump, ungerminated sclerotia were found among the debris along the shore of Lyngby Sö long after the last apothecia had disappeared. On the other hand, these sclerotia may not be capable of germination for some unknown reason.

The germinability of the sclerotia may be conditioned in some way by the functioning of the spermatia. The writer's original suggestion (Whetzel 1929: 18) that the microconidia probably function as do the spermatia of the rusts has since been supported by the work of Drayton (1934) in his work on *Sclerotinia gladioli*. Ferdinandsen & Winge (1911: 297) think the microconidia may function as true conidia, causing secondary infections later in the season when primary infections by ascospores are no longer possible. This seems very doubtful though they cite some observations in support of this hypothesis. The writer has had no satisfactory opportunity to attempt a careful study of the germination and role of the spermatia, but believes that *S. scirpicola* is a favorable species for such an investigation. It occurs in great abundance in Lyngby within easy walking distance of excellent laboratory facilities. It is to be hoped that Professor Ferdinandsen or some of his students will undertake intensive investigation on this very interesting and important problem, as they are most favorably situated for such an undertaking.

The suggestion of Ferdinandsen and Winge that invasion by the fungus takes place through the culm at some point just below the inflorescence does not appear tenable. Ascospores shot on to culms at this point, in moist chambers, were observed to germinate poorly or to produce spermatia only. No germ tubes could be found penetrating the epidermis or entering through the stomata, which are numerous all over the culm, while actual invasion of the stigmas was easily demonstrated. The death of the pedicles of infected spikes prior to the first evidences of infection in the culm itself also argues for blossom invasion. While the very limited and preliminary

investigations which we have been able to make all point definitely to the pistils of the *Scirpus* as the infection court, more extensive studies and inoculation experiments should be made.

ORIGIN AND RELATIONSHIPS

Undoubtedly *Sclerotinia scirpicola* is very closely related to the species on *Carex*. It differs from these chiefly in the characters of its spermodochidia and sclerotia. On the whole, it approaches more nearly *S. sulcata* rather than *S. duriaeana*, as suggested by Ferdinandsen and Winge who, however, at that time were not aware of the fact that there were two distinct species confused under the name *S. duriaeana*. Its similarity to *S. sulcata* is most marked in its cultural characters. Its dense cottony growth of aerial mycelium and large tuberoid sclerotia produced on potato dextrose agar are scarcely to be distinguished from those produced by *S. sulcata* in pure cultures. Sclerotial production on potato dextrose agar is, however, much more tardy and less certain, while the growth of aerial mycelium is generally more abundant; the submerged mycelium is also more promptly and extensively darkened. Its spermodochidial patches also simulate those of *S. sulcata* in their irregular distribution on the culm. The form of its sclerotia in nature is quite distinct but may possibly be due entirely to the structure of the *Scirpus* culm. It is probably restricted in its pathogenism to *Scirpus*. Many *Carex* species were common about the shores of Lyngby Sö, but only two or three apothecia arising from sclerotia of the *Carex* type were found among the apothecia of *S. scirpicola* along the lake shore. Cultures from one of these proved to be typical of *S. duriaeana*. Infected culms of *C. disticha* in the same locality yielded typical cultures of *S. sulcata*. Moreover, the period of apothecial development is distinctly later for *S. scirpicola* than for the species on *Carex*. Apothecia of the species on *Carex* were rarely to be found about Lyngby when we arrived at the beginning of June, although infection of the culms of *C. Hudsonii* by *S. sulcata* were discovered in abundance shortly after our arrival. The blossoming period for *Carex* species was also practically past. Since two to three weeks are required for the development of visible infection after inoculation by *S. duriaeana* or *S. sulcata* in their *Carex* suscepts, the scarcity of apothecia of these species when those of *S. scirpicola* were at their optimum abundance is significant In spite of all this evidence as to the specific identity of *S. scirpicola*, careful cross inoculation experiments should be made with this form on species of *Carex* known to be suscepts for *S. sulcata* and *S. duriaeana*. Here is another interesting problem for some energetic young pathologist or mycologist who can avail himself of the exceptional opportunity afforded there at Lyngby.

The marked similarity of *S. scirpicola* to *S. sulcata* appears to be of considerable significance in connection with my theory of the origin and evolution of this group of species on cyperaceous suscepts. It would seem that *S. scirpicola* has been a relatively recent differentiation derived directly from the European form of *S. sulcata*, which is probably also the mother

PLATE IX

species of *S. duriaeana*. The characters peculiar to *S. scirpicola* may, in part at least, be due to its adaptations to a different suscept.

While Mougeot is credited by Fries with having first applied the name *Sclerotium roseum* to the original collecton made by Kneiff, there is substantial evidence that Kneiff himself is the legitimate author of the name. Not only did Mougeot and Nestler credit Kneiff with this name on the label of their Stirp. Crypt. Vogeso-Rhen. *884* (1826), but also Kneiff and Hartmann, two years later, in distributing this sclerotial stage, in their Pl. Crypt. Badens *20*, credit the name to Kneiff. Subsequent writers in referring to this name are divided as to the legitimate author of it. Tulasne and others follow Fries, but most of them credit Kneiff with the name. Saccardo (1899: 1153) notes that the name "*Sclerotium Kneiffi*" is applied to this fungus by others ("Quibusdam"). I have been unable to locate any other reference to the fungus under this name.

Currey's assumption (1857) that "*Sclerotium roseum* Kneiff" is the sclerotial stage of "*Peziza curreyana*" was accepted by all subsequent students of *S. curreyana* until Rehm (1893) pointed out the error in the note to his description of *Sclerotinia scirpicola*. This confusion of the sclerotia in the culms of *Scirpus* with those in the culms of *Juncus* as representing one and the same species had not, however, escaped suspicion in the critical mind of Tulasne (1861: 105) who while admitting that the sclerotium in *Scirpus* ". . . seems to agree completely with it (in Juncus) in its whole structure though no one has yet found it in fruit" remarks "But we are sorry that it has not been possible for us to test it by suitable culture, for we have never seen it alive".

SCLEROTINIA SCHOENICOLA

PLATE IX, FIGS. 36–38

Desmazières appears to have been the only mycologist to refer to specimens of what proves to be a heretofore unrecognized species of *Sclerotinia*. He took the sclerotial and spermatial stages of this fungus on *Schoenus nigricans* (Figs. 36–38) to be the same as those on species of *Carex* which he designated respectively *Sclerotium sulcatum* and *Epidocium affine*, and which were later (1929) recognized by Whetzel as stages in the life cycle of *Sclerotinia sulcata*.

Desmazières [7] distributed specimens of the culms of *Carex vulpina* and *acuta* and culms of *Schoenus nigricans* all of which contained sclerotia very

[7] Plantes Cryptogames France, Ed. 1, Ser. I, No. *2029* (1850); Ed. 2, Ser. II, No. *1629* (1853).

Plate 9. *Sclerotinia schoenicola* and *S. luzulae*. **Fig. 36.** Culms of *Schoenus nigricans* showing spermodochidial patches, from Desmazières' Plantes Crypt. France, Ser. II, *21*; about natural size. **Fig. 37.** Spermodochidial areas, x6. **Fig. 38.** Sclerotia of *S. schoenicola* from culms of *Schoenus nigricans* from Desmazières' Plantes Crypt. France, Ed. 2, Ser. I, *1629*; natural size. **Fig. 39.** Culms of *Luzula pilosa* from Krieger's Fung. Sax. *2073* showing sclerotia of *Sclerotinia luzulae* (revived dry specimens); natural size. **Fig. 40.** Portions of a sclerotium still enclosed in the culm, x6.

similar in character (see Whetzel 1929: 7) and which he collectively labeled "Sclerotium sulcatum Rob. in herb." No date or locality is indicated on the packets. Presumably Roberge was the collector. In specimen *2029* the culms were all mixed together. In his formal description of *Sclerotium sulcatum*, Desmazières (1851) does not mention *Schoenus nigricans* specifically, saying only "hab. in culmis siccis Caricum"; but in the note following he says (transl.) "This fungus was found inside triangular stubble of *Carex vulpina* and *C. acuta* and in species with cylindrical culms", the last referring undoubtedly to *S. nigricans* which, in the later distributed specimens (number *1629*), were segregated into a separate packet and labeled *Schoenus nigricans*. His description clearly applies primarily to the sclerotia in the *Carex* culms, thus in effect leaving those in *S. nigricans* without a name.

Desmazières [8] later (1853) distributed the upper portions of the same culms containing the spermatial fruit bodies as those containing the sclerotia (Ed. 1, Ser. I, *2029*; Ed. 2, Ser. II, *1629*) distributed in 1850. Here, however, he separated the culms of *Schoenus* from those of *Carex* in different packets. In his description of the spermatial fruit bodies (1853) he gives these the name "Epidocium affine Desmaz." and gives both *Schoenus nigricans* and *Carex* species as suscepts citing his exsiccati specimens Series II, *21*. His description, however, clearly applies primarily to the fruit bodies on the *Carex* culms, thus again leaving those on *Schoenus* nameless.

The evidence clearly indicates that the sclerotia and the spermodochidia on *Schoenus nigricans* belong to the same fungus. The spermodochidial patches on the culms of *S. nigricans* are quite distinct in character from those of *E. affine* and from those of the other *Sclerotinia* species on the *Cyperaceae*. (Compare Figs. 36 and 37 with Figs. 11–14.) The sclerotia, while very similar to those of *S. sulcata*, are rather more slender but the spermodochidia are very different. Since the spermodochidia are taxonomically the most distinctive structures of the different species of *Sclerotinia* in this group, I have no hesitation in giving to this species a distinctive name.

It is perhaps remarkable that this species apparently has not been collected by mycologists since the days of Desmazières. It is probably not rare but will be found by one seeking it in the proper localities. I unfortunately encountered *Schoenus nigricans* in but one locality in Europe. That was in late summer on the fens at King's Lynn, England. No trace of the *Sclerotinia* was found.

This species is here presented, chiefly to bring it to the attention of European mycologists in the hope that someone will be stimulated again to discover this very interesting form and make a more complete study of its different stages. Only in this way may it be determined whether I am correct in assuming it to be distinct from other species occurring on members of the *Cyperaceae*. Our present scanty knowledge of this form is summarized in the following technical description.

[8] Plantes Cryptogames France, Ed. 3, Ser. II, No. *21* (1853).

SCLEROTINIA SCHOENICOLA, sp. nov.

Maculis spermodochidialibus majusculis, ovatis vel circularibus, numerosis, magnitudine variabilibus, 2–6 mm. in diametro, sub inflorescentiis infectis irregulariter secundum unum culmi latus dispositis, pallide olivaceo-brunneis coloris atroolivacei massae spermodochidiorum globosorum luridequeque brunnei cellularum contextus suscipientis gratia; structura interna spermodochidiorum structurae *S. scirpicolae* subsimili; sclerotiis gracilibus, fusiformibus, apicibus obtusis instructis, strictis, rarius manifeste curvatis vel inaequilateralibus sclerotiorum *S. sulcatae* modo, initio pallide roseis, dein nigrescentibus ad superficiem, intus albis, fortiter arato-sulcatis, 8–10 x 1–2 mm. in statu sicco, per rimam culmi liberatis; apotheciis ignotis.

Spermodochidial patches (Figs. 36, 37) rather large, ovate to circular, numerous, variable in size, 2–6 mm. diam., distributed irregularly along one side of the cylindrical culm, just below the blighted head, pale olivaceous brown, due to the dark olivaceous color of the massed globose spermodochia and dead brown cells of the suscept tissues; internal structure essentially like that of the spermodochidia of *S. scirpicola*.

Sclerotia (Fig. 38) slender, fusiform, tips blunt, straight, rarely distinctly curved or inequilateral as are the sclerotia of *S. sulcata*, at first pale pink, becoming black externally, white within, strongly furrowed, 8–10 mm. long by 1–2 mm. thick (dry), discharged by a slit in the culm.

Apothecia unknown.

HABITAT: Culms of *Schoenus nigricans* L.

DISTRIBUTION: Apparently known only from France. There is nothing on the labels of Desmazières' specimens (the three cited above) to indicate where, when, and by whom they were collected. All were presumably from material sent him by Roberge.

TYPE SPECIMENS: Desm. Pl. Crypt. France. Ed. 1, Ser. I, *2029* (in part) (1850), and Ed. 2, Ser. II, *1629* (in part) (1853), (sclerotia only); Ed. 3, Ser. II, *21* (in part) (1853) (spermodochidia only).

SPECIMENS EXAMINED: The specimens from Desmazières' Plantes Cryptogames France listed above were examined in the Royal Herbarium at Kew and in the British Museum in London, in the New York Botanical Gardens, in the Farlow Herbarium, Cambridge, Mass., and in the Mycological Collections, Bur. Pl. Ind., U.S.D.A.

The life history of *S. schoenicola* is presumably similar to that of the other species of *Sclerotinia* attacking cyperaceous suscepts. Invasion is evidently by way of the flowers. The appearance of the spermodochidia might suggest a near relationship to *S. scirpicola*, while from the shape and size of the sclerotia one would rather infer that *S. schoenicola* is more nearly related to *S. duriaeana* or *S. sulcata*.

SPECIES ON THE JUNCACEAE

There are, as far as I have discovered, but three species of the true *Sclerotinias* attacking members of the Juncaceae. These are *S. curreyana*, very common in culms of *Juncus effusus* in Great Britain and western continental Europe; a species in our Pacific Northwest, described as *Ciboria juncigena*; and an undescribed species on *Luzula pilosa* known only from one collection taken in Saxony, Germany.

PLATE X

SCLEROTINIA CURREYANA

PLATE X AND TEXT FIG. D

Tulasne in 1861 in his Selecta Fungorum Carpologia (**1:** 104–105) described accurately and in some detail two species of *Sclerotinia* in the group under consideration in this paper, and in 1865 (**3:** pl. 22) presented beautiful illustrations of both.

Thus *S. curreyana* and *S. duriaeana* may well be regarded as the classical representatives of the species of *Sclerotinia* occurring on sedges and rushes. Of these two, *S. curreyana* has long been the best known to the English and European mycologists since the time of its study by Berkeley and Currey in 1857, because of its very common occurrence and the fact that the apothecia are readily found arising from the sclerotia of the still standing, bleached culms. There is strong circumstantial evidence, however, that it was really first described by Fries in 1818 under the name of *Peziza ciborioides*. Rehm (1893: 822) appears to have been the first to question whether *Peziza ciborioides* of Fries (1824), to which Persoon four years later (1822: 277) gave the new name *Peziza friesii*, may not have been the *Peziza curreyana* which Currey described in 1857. A careful consideration of all the evidence leads me to believe that Fries actually had this species on culms of *Juncus* in view when he named and described *P. ciborioides*. His description fits the species well, inadequate though it is. The fact that his fungus occurred in culms in early spring in marshy places is very suggestive if not confirmatory evidence for my opinion. However, since Fries' specimens are not preserved and since the fungus is so well known under the name suggested by Berkeley, I am not using the Friesian name which current rules of nomenclature might justify. I found this species very abundant in the region about London in the early spring of 1930 and so had an unusual opportunity to observe and study it. I have searched for it diligently since that time on *Juncus effusus* in the Cayuga Lake region of central New York, but have never found it, nor is it recorded from anywhere in North America, unless *S. juncigena* should prove to be conspecific. It should be found throughout the Euro-Asian continent wherever its suscepts occur.

SCLEROTINIA CURREYANA (Berk. *in* Currey) Karsten, Revisio Monogr. p. 123. 1885.

Peziza curreyana Berk. *in* Currey, Journ. Linn. Soc. **1:** 147. 1857.
Peziza curreyi Berk. Outlines Brit. Fung. p. 370. 1860.
Rutstroemia curreyana Karst. Myc. Fenn. **1:** 107. 1871.
Phialea curreyana (Bart.) Gillet, Discom. p. 211. 1879.
Sphacelia tenella Sacc. Miscellanea Mycologica *in* Venezia Ist. Atti, Ser. 6, **2:** 448. (Reprint **1:** 14) 1884. (See Saccardo 1886: 666.)

Plate 10. *Sclerotinia curreyana*. **Fig. 41.** Diseased culms of *Juncus effusus* showing spermodochidia; about natural size. CUPP *31655*. **Fig. 42.** Spermodochidia, x6. **Fig. 43.** Apothecia arising from sclerotia within standing culm; natural size. CUPP *15578*. **Fig. 44.** Apothecia in various stages of development from sclerotia in culms in moist chamber; natural size. CUPP *20198*. **Fig. 45.** Apothecia fully expanded; culms showing rupture slits over enclosed sclerotia, x2. CUPP *20198*.

Peziza juncifida Nylander, Pezizas Fenniae *in* Sällsk. Fauna et Fl. Fenn. Forhändl. Notiser (n. s. 7) **10:** 39. 1869.
Hymenocypha curreyana Phill. Manual Brit. Discom. p. 16. 1887.
Placosphaeria junci Bubák, Ann. Myc. **4:** 113–114. 1906.
Sphacelia curreyana Grove, Journ. Bot. Brit. and Foreign **50:** 46. 1912.
Myrioconium tenellum V. Höhnel, Mitteil. Bot. Inst. Tech. Hochsch. Wien. **3:** 50. 1926.

Spermodochidia (Figs. 41, 42) numerous, scattered irregularly along and about the upper part of the diseased culms, usually most numerous along one-half of the circumference of the culm, minute, pustulate, ellipsoid, brown, slightly erumpent when fresh and moist, opening by a slit in the epidermis; *spermatia* minute, globose, 2–2.5 μ in diameter, produced from the tips of obclavate spermatophores fasciculately clustered about a centrum to form globose spermodochia as in other species of this group, but also forming an irregular hymenium lining the cavity.

Sclerotia one to several in each culm, short, stout, cylindric with blunt, rounded ends, 4–15 mm. or more long, by 2–4 mm. in diameter, externally black or dark brown, coarsely sulcate, internally white when mature, of a rosy pink color during development, embedded in the pithy interior of the culm, disclosing in section the inclusion here and there of remnants of undigested pith cells. The structure of the rind and medulla is essentially like that of the sclerotia of *S. scirpicola*. The sclerotia are not freed from the culms at maturity but remain embedded, apothecia developing in the spring from the surface exposed by a slit in the epidermis of the culm over the sclerotium.

Apothecia (Figs. 43–45) two to several from each sclerotium, short-stipitate, pale tan to dark avellaneous brown; *cup* thin, deep goblet-shaped to infundibuliform, often umbilicate, 2–12 mm. or more in diameter, margin entire, recurved, smooth without, rugose-fluted within; *stipe* as long as the diameter of the cup, equally cylindrical, flexuous, solid, glabrous or slightly hairy to tomentose at the base, somewhat darker in color than the cup; *asci* long, slender, clavate, apex rounded, 38 meas. gave 47.6–78 x 4–5.4 μ, mode 65 x 5.4 μ, av. 65.2 x 5 μ; 8-spored, spores uniseriate; *ascospores* slender, allantoid, ends rounded, 99 meas. gave 7.9–14.5 x 1.3–2.9 μ, mode 11 x 2.9 μ, av. 11.5 x 2.5 μ; *paraphyses* "slender, pale brown at the slightly thickened apex", according to Massee (1895: 282). I have found it impossible satisfactorily to make out the characters of the paraphyses from dry material.

In culture on potato dextrose agar this fungus makes a dense cottony, felty growth of pinkish aerial mycelium with eventual development therein of more or less globose sclerotia which are at first a bright pink, and finally form a white to pink medulla that is enclosed in an olivaceous brown rind. The olivaceous brown masses of sporodochia form about the margin of the mycelial mat.

HABITAT: In culms of *Juncus*, most common in *Juncus effusus* L. but recorded also on *J. conglomeratus* L., *J. glaucus* Ehrh., and *J. filiformis* L.

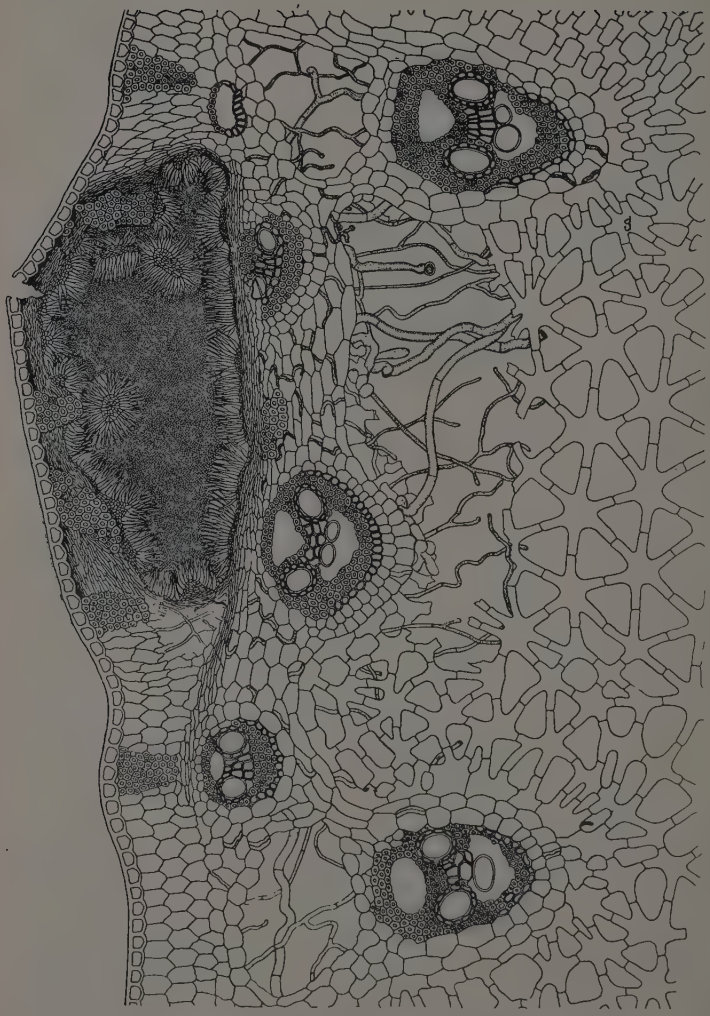
in wet locations, meadows, heaths, moors, and along ditches. The apothecia appear in early spring, followed by infection of the culms in which the spermatia and sclerotia appear during midsummer and early autumn.

DISTRIBUTION: This species appears to be most common in Great Britain judging from my own observations and from the numerous collections in herbaria. Known also from Belgium (Lambotte 1887: 303) and Bommer and Rousseau (1884: 133), France (Boudier 1905: 273–4) and Saccardo (1889: 199), Finland (Nylander 1869: 39), Denmark (Lind 1913: 109), Bohemia (Bubák 1906: 113, spermodochidia). Velenovsky (1934: 223) records this species in Bohemia on *Juncus glaucus* and *J. piscinam*, also in heads of wheat. His description and his figures would indicate that he had some species quite different from *S. curreyana*. The spores as he describes and figures them are certainly not the spores of this species.

TYPE SPECIMEN: There are a number of collections of this species deposited (in 1881) in the Royal Herbarium at Kew of which at least three packets are from Currey's personal herbarium and collected on "Paul's Cray Common, Near Chislehurst in Kent", the locality given by Currey (1857) as the place where, on the 23rd of April 1856, he first discovered the apothecia of *Peziza curreyana*. The label on these specimens says "On *Juncus conglomeratus*" and is dated "May, 1856". These specimens would, therefore, appear to constitute the type material. Massee (1895: 283) says that he had examined the type specimen.

MATERIAL EXAMINED: In addition to Currey's type specimens, I have carefully examined the other twelve specimens in the Kew Herbarium, all of which were apparently collected in England from 1856 to 1884. The labels for most of them are very sketchy. They appear to be mostly specimens collected by (or sent to) Currey and Berkeley. In the herbarium of the British Museum there is a sheet and a half of packets of this species, all originally in the collection of William Phillips. One specimen labeled "conidia" is of special interest, as showing that Phillips recognized the spermatial stage of *S. curreyana*. These all appear to have been collected in England.

In addition to the above, I have had for study the following: On **Juncus effusus** L.: CUPP *15578*, Worcester, England, October 18, 1926, *C. Rea* (sclerotia from which I developed apothecia the following April); — CUPP *31648*, Wisley, Surrey, England, February 10, 1930, *Whetzel, Green & Cotton* (apothecia); — CUPP *31654*, Goslar am Harz, Germany, Harzerberger Thal, *Whetzel & Westcott*, April 22, 1930 (apothecia); — CUPP *31655*, near Downton in Hampshire, England, August 2, 1930, *Whetzel & Brown* (spermodochidia); — CUPP *31657*, Sandhill bog, Worcestershire, England, August 9, 1930, *Whetzel & Rea* (spermodochidia and sclerotia). On **Juncus conglomeratus** L.: CUPP *31658*, shore of Loch Katrine near Stronachlar Pier, Scotland, August 3, 1930, *Mrs. Whetzel & Miss Westcott* (spermodochidia); — CUPP *31659*, near Plowright's old home, not far from King's Lynn, England, *Whetzel* (spermodochidia); — CUPP *20198*, Phytopathological Field Station, Slough, Buckingham, England, December 5, 1931, *Mr. and Mrs. E. W. Mason* (sclerotia from which I developed apothecia in April at Ithaca, New York); — CUPP *31662*, near London, England, May 1934, *William Brown* (sclerotia); — Otto Jaap, Fungi Selecti Exs. *754 a* and *b*. Prov. Brandenburg, Triglitz in Prignitz, *O. Jaap*. (a) apothecia, May 30, 1916. (b) spermodochidia, "Placosphaeria junci", *Bubák*, November 3, 1915; — CUPP *31656*, near Downton, Hampshire, England, August 2, 1930, *Whetzel & William Brown* (spermodochidia); — Sydow, Mycotheca germanica *2358*, near Burgholdinghausen, Kreis Siegen, Westfalen, Germany, May 18, 1924, *A. Ludwig* (apothecia).



TEXT FIG. D

This species is also said to occur on *Juncus glaucus* Ehrh., on *J. filiformis* L. and on *J. communis* E. May. Saccardo (1886: 666) described the spermatial stage under the name *Sphacelia tenella* from a collection on *Juncus glaucus* collected near Rouen, France. Mr. Carleton Rea (in a letter April 24, 1927) says the sclerotia of *S. curreyana* are common in the culms of this species in the vicinity of Worcester, England. Bubák (1906: 113) described what is apparently the spermatial stage of our fungus under the name *Placosphaeria junci* in culms of *Juncus filiformis* and Nylander (1869) has described the apothecial stage under the name *Peziza juncifida* on culms of *Juncus* (*compressi?*) but I have not seen material on any of these suscepts.

In numerous records of collections of this fungus, the species of *Juncus* on which it occurred is not given. The evidence available seems to indicate very clearly that *S. curreyana* is most frequently to be found on *Juncus effusus* L. and *Juncus conglomeratus* L.

The erroneous identification of the sclerotial stage of *S. curreyana* with that of *S. scirpicola* by Currey and Berkeley has resulted in the citation of *Sclerotium roseum* in many synonymies of *S. curreyana* (See p. 413). In his transfer of *Peziza curreyana* to the genus *Phialea*, Gillet writes "Bart." for the author of the species. This appears to be an error for "Berk." The inclusion of *Peziza juncifida* Nyl. and *Placosphaeria junci* Bubák in the synonymy of this species might be questioned, since I have not been able to see authentic specimens of either. Nylander's description of *P. juncifida*, while brief, appears to me to justify the conclusion that he had apothecia of *S. curreyana* in hand.

There would appear to be little question of the identity of Bubák's fungus with the spermatial stage of *S. curreyana*, since his sketch of a section through the fruit body is quite in character with the spermodochidium of this Discomycete (See Text Fig. D.) Bubák records his fungus on *Juncus filiformis*, a species on which this Discomycete is not otherwise known to occur.

The slender curved ascospores of *S. curreyana* are strikingly different from the ascospores of any of the other species in the genus. The structure of the spermodochidium is also different from that of the others. The dark color is due in part to the dilute brownish color of the central hyphae of the spermodochidia and brown hyphae in the covering epidermal cells. It is, however, largely the result of the dark brown discoloration of the crushed thin-walled cells of the parenchyma surrounding the spermodochidial cavity giving the appearance of a spermogonial wall. This "wall" is further suggestive of a true hyphal wall, since resting upon it is a spermatophore hymenium, lining the cavity (Text Fig. D). This hymenial lining presents a picture very different from that in the spermodochidia of the species in *Carex* suscepts, where it is entirely wanting. However, just as in the *Carex*-

Text Fig. D. Cross section through a spermodochidium of *Sclerotinia curreyana* about x200. Note that the cavity is formed by extensive lysis of the parenchyma between the vascular bundles with collapse and browning of the surrounding cells to form a pseudo-spermogonial wall. Drawn by Carlos Garcés.

invading species, *S. curreyana* also produces globose spermodochidia which lie typically in the central cavity of the hymenium-lined spermodochidium. These peculiarities might be taken to indicate that it is not closely related to the other species in the group here under consideration, but in all its other characters it conforms very closely. Its nearest relationship would seem to be with *S. scirpicola* if one considers the similarity of the sclerotia of these two species.

In culture on potato dextrose agar *S. curreyana* presents a picture strikingly like that of *S. sulcata*, the chief difference being the pinker hue of the mycelial mat of the former. Both form sclerotia on this medium and the medulla of the sclerotium of *S. sulcata* is nearly as pink as that of *S. curreyana* at comparable stages in its development.

It is remarkable in the light of Tulasne's recognition (1861: 104) of the spermatial stage in *S. duriaeana* that the spermatial stage of *S. curreyana* was not described until 1884 (Saccardo) and not recognized as such until 1912 (Grove). Grove says the spermatia measure 3–5 μ in diameter. Presumably his measurements were made from fresh material. Mine (2–2.5 μ) were made under oil immersion from dry material soaked over night in weak KOH. This difference in size is, however, hard to explain on these grounds.

SCLEROTINIA JUNCIGENA

In May 1883, Suksdorf collected the apothecial stage of a little Discomycete apparently growing on the surface of "dead stems of *Juncus* above the water in Falcon Valley", according to a note on the packets distributed by him in his exsiccati, Flora of Washington. Ellis, who determined the material, gave it the name *Ciboria juncigena* E. & E. Dr. J. R. Keinholz advises me in a letter of June 7, 1942 that the name "Falcon Valley" apparently was abandoned many years ago and the name changed to "Hell Roaring Meadows", which lies at the head of a creek of the same name. No other collections of this form have been preserved as far as I can discover, although Dr. S. M. Zeller of the Oregon Experiment Station writes me that he has once come upon this fungus in the field. The species of *Juncus* is not given by Suksdorf but it is probably *J. effusus* var. *pacificus* Fern. & Wiegand. Dr. Keinholz who kindly undertook to locate fresh material of this fungus has thus far been unsuccessful. Its close resemblance to *S. curreyana* of Europe makes a critical study of living specimens highly desirable. Pending such a study it seems wisest to retain its present specific standing.

SCLEROTINIA JUNCIGENA (E. & E.) n. comb.

Ciboria juncigena E. & E., Proc. Acad. Nat. Sci. Phila., Nov. 30, 1894, p. 348.

Spermodochidia not seen.

Sclerotia one, possibly more, within a diseased culm, slender, cylindric, with truncate, slightly rounded ends, up to 15 mm. long by 2 mm. in diameter, externally black, finely sulcate, internally white when mature; apparently lying free in a lysigenous cavity in the pith region of the culm; structure essentially like that of *S. curreyana*. The sclerotia are not freed from

the culm at maturity, nor are they apparently exposed by a slit on emergence of the apothecia as in *S. curreyana.*

Apothecia usually but one from each sclerotium, long-stipitate, avellaneous (?); *cup* thin, membranous, shallow cup-shaped, sub-umbilicate, 4–5 mm. in diameter; *hymenium* "wine colored"; *stipe* arising from the sclerotium within and penetrating the wall of the culm, relatively long, about 1 cm. by 1 mm. thick, lower half or more black, longitudinally wrinkled, fibrillose, anchored at point of emergence to the surface of the culm by a spreading dark hyphal mat, concolorous above with the cup; *asci* clavate-cylindrical, (Ellis meas.) about 60 x 4–5 μ, 8-spored, spores sub-biseriate; *ascospores* allantoid, slender, distinctly curved, hyaline, (Ellis meas.) 7–8 x 1.25 μ, (Whetzel, 50 meas. in KOH) 7.2–10.8 x 1.2–2.4 μ, mode 8.4 x 2.4 μ, average 8.86 x 1.83 μ; *paraphyses* not distinguishable in mounts from dried material.

HABITAT: In culms of *Juncus* (probably *J. effusus* L. var. *californicus* Fern. & Wiegand) in wet marshes. The apothecia appear in May on standing dead culms.

DISTRIBUTION: Known only from the type locality. Falcon Valley (now Hell Roaring Meadows), Washington State.

TYPE SPECIMEN: Exsiccati specimens distributed as *371* Flora of Washington. Collected by W. N. Suksdorf, May 31, 1883. I have seen two packets, one deposited from the Ellis Collection in the N. Y. Bot. Gard. herbarium and another in the Mycol. Coll. Bur. Pl. Ind., Washington, D. C.

It is with some hesitation that I treat *Ciboria juncigena* E. & E. as a species distinct from *S. curreyana.* It is undoubtedly a *Sclerotinia* rather than a *Ciboria.* Ellis entirely overlooked the presence of the sclerotia, which was perhaps due to the absence of a slit in the culm over the sclerotium and the unusual anchorage of the stipe to the surface of the culm. As far as the characters of the cup are concerned, it could hardly be distinguished from *S. curreyana,* but the long, slender stipe, its black color, and the basal, dark hyphal mat anchoring it to the culm at the point of emergence, together with the slender character of the sclerotium, may well prove to be dependable evidence of its specific character. It is unquestionably very closely related to *S. curreyana* and may indeed be more properly regarded as an American form of variety of that species. However, my experience with the closely related *S. duriaeana* and *S. sulcata,* together with the fact of its long geographical isolation from the ancestral *S. curreyana,* inclines me to believe that a fuller study of *S. juncigena* in fresh condition and in its spermatial stage will prove it to be a distinct species.

SPECIES ON LUZULA

SCLEROTINIA LUZULAE

PLATE IX, FIGS. 39 AND 40

W. Krieger distributed in his Fungi Saxonici *2073* culms of *Luzula pilosa* L. in which are embedded slender black sclerotia of a fungus which he

labeled provisionally "*?Sclerotinia Curreyana* (Berk.) Karst." The label bears a brief description of the sclerotia with the remark that unfortunately he had been unable to develop the fruit body of the Ascomycete, hence the question mark before the name he was giving the specimen. He apparently collected the specimens he distributed under this number in two different localities and in different years, in Polenztale, Utterwaldergrunde, late May 1896, and near Königstein, June 1897. In Rehm's collections at Stockholm, Sweden, there is in addition to Krieger's exsiccati specimen *2073*, another packet labeled in Krieger's handwriting bearing the same data, evidently duplicate material.

I have been able to locate but one other collection which is in the herbarium of the Mycological Collections, Bur. Pl. Ind., U. S. D. A., Washington, D. C. This bears the label "Herbarium G. Bresadola, *221* Sclerotium roseum Moug. en feo oritur Scler. Curreyana Berk. Sclerotium Luzulae Krieg. n. sp.? In den dürren Halmen von Luzula pilosa Willd. bei Königstein, 19. Juli, 1897. Lg. W. Krieger". The name "*Sclerotium luzulae* Krieg." appears never to have been published. The specimen is apparently a part of the 1897 collection distributed by Krieger in his Fungi Saxonici *2073*. Krieger's collections of a sclerotial form on *Luzula pilosa* would seem, for the present, best regarded as a distinct species.

SCLEROTINIA LUZULAE sp. nov.

Spermodochidiis apparenter nullis; sclerotiis 1–3 vel pluribus, intra culmos natis et maturitate ad superficiem soli ruptionis culmorum causa liberatis, 5–30 x 1 mm., fusiformibus, acute abrupteque acuminatis unum ad latus, aqua imbutis obscure castaneis, siccis nigris, indistincte arato-sulcatis, cortice uno e strato cellularum atro-tunictarum consistente, medulla alba, ex hyphis dense compactis, multo minoribus diametro ordinario specierum stirpis huius composita; apotheciis ignotis.

Spermodochidia apparently wanting.

Sclerotia one to three or more formed within the culms which are ruptured at maturity, discharging the sclerotia onto the soil, 5–30 mm. long by 1 mm. in diameter, fusiform, sharply and abruptly pointed at either end, dark mahogany brown when soaked in water, black when dry, indistinctly furrowed, not sulcate as in other species in this group, rind one layer of dark-walled cells, medulla white, composed of densely packed hyphae which are much smaller in diameter than those of the sclerotia of other species in this group.

Apothecia unknown.

HABITAT: In culms of *Luzula pilosa* Willd. in Saxony, Germany.

DISTRIBUTION: Known only from the type locality and very rare, according to the collector.

TYPE SPECIMEN: Krieger's Fungi Saxonici *2073*, in culms of *Luzula pilosa* Willd. in Polenztale, Utterwaldergrunde, May 1896 and near Königstein, June 1897, *W. Krieger.*

MATERIAL EXAMINED: I have carefully examined the specimens of the type collections in the British Museum and in the CUPP Herbarium; also the specimen from the herbarium of the Bur. Pl. Ind., U.S.D.A.

Krieger, on the label of his Fungi Saxonici *2073*, refers the specimen provisionally to *Sclerotinia curreyana* and cites *Sclerotium roseum* Fr. as a synonym, obviously two errors. This species is probably more common than Krieger surmises and should be sought wherever the suscept occurs.

The apparently complete absence of spermatial fruit bodies is puzzling. I have scrutinized carefully all the culms which I find in Krieger's collections but without finding any trace of spermodochidia. Their absence is most unusual, this being the only species in this group, except *S. vahliana* and *S. juncigena*, in which I have not found them. That I should have found them in these two species is almost certain had I had specimens of diseased culms collected during the summer.

EXCLUDED SPECIES

Several species of stromatic Discomycetes other than those described above occurring on species of the *Cyperaceae* and *Juncaceae* have been put in the genus *Sclerotinia* by various authors. None of these species with which I am acquainted are, however, congeneric with the true species of *Sclerotinia* as I interpret that genus. I list them here with some observations and comments which may prove useful to my mycological colleagues until such time as I may treat them more fully.

Sclerotinia aschersoniana P. Henn. & Plöttn. Verh. Bot. Vereins, Prov. Brandenburg **41:** IX, 1899.

This species is pathogenic in the ovaries of certain species of *Carex*, notably in *C. hudsonii* A. Bennet (=*C. stricta* Good.) in Europe and on *C. stricta* Lam. in North America. I have collected and cultured it frequently from the latter species in swamps in central New York and once from *C. prairea* Dewey in the same region. It is certainly not a *Sclerotinia*. It infects the suscept by ascospore invasion through the stigma, converting the ovary into a black stromatized mummy. It might be referred to the genus *Ciboria* but its proper taxonomic relationships require further consideration.

Sclerotinia utriculorum Boud. Bull. Soc. Myc. France **19:** 196–197, *pl. 8, fig. 6*. 1903.

This is described as growing on the hard seeds of *Carex davalliana* in May, in the Jura in France. Boudier says it differs from other species of *Sclerotinia* on *Carex* in that the apothecia do not arise from sclerotia but from the sclerified achenes of the *Carex*. As he makes no reference to *S. aschersoniana* it is probable he was unaware of that species. As far as I can judge, *S. utriculorum* Boud. is specifically the same as *S. aschersoniana* P. Henn. & Plöttn. Velenovsky (1934: 224) apparently regards this species as identical with *S. aschersoniana*, citing the latter as a synonym of *S. utriculorum*, but his reason for this is not clear.

Sclerotinia vesicariae Giesenhagen, Ber. Bayer. Gesell. Erforsch. der Heim. Flora **11:** 167–169. 1907.

This species is said to occur among ("inter") fallen dead seed of *Carex vesicariae* in autumn, collected by Stechsee near Seehaupt, Bavaria. The sclerotia are said to be irregularly cylindrical, rough, black, white within, 5–8 mm. long by 2 mm. in diameter. This would seem to indicate that this species does not occur in the ovaries of the *Carex*, but there is little else to indicate that it is distinct from *S. aschersoniana*. The asci are said to be 180–190 μ, considerably longer than those of *S. aschersoniana* which are given as 90–110 μ in the original description; the width is about the same. Ascus measurements, however, are so very variable in the stromatic Discomycetes, especially the length, as to be of little specific significance. The size and shape of the spores approximates those of *S. aschersoniana*. I am inclined to regard *S. vesicariae* as specifically distinct.

Sclerotinia caricina Velenovsky, Monog. Discom. Bohemiae **1:** 224; **2:** *pl. 22, fig. 40.* 1934.

This species is said to occur on the roots of *Carex muricata* among *Juncus communis*. It is not possible to tell from Velenovsky's description and figure whether this is a true *Sclerotinia* or not.

Sclerotinia paludosa Davidson & Cash, Mycologia **25:** 271. 1933.

A critical examination of all the specimens on which this species is based, discloses that the sclerotia shown in their *fig. 7* are those of a *Typhula*. The apothecia in the other specimens do not arise from sclerotia but from stromatized leaf tissues. This fungus is undoubtedly a *Rutstroemia*. It is a common species of wide distribution occurring on leaves and culms of various species of sedges, grasses, etc. The proper species name remains to be determined. It is probably conspecific with the following species.

Sclerotinia heterocarpa Bennett, Ann. Appl. Biol. **24:** 254. 1937.

While this species is described as occurring on grasses as the cause of the "dollar-spot" of turf, what is without doubt the same species has been discovered by the writer on leaves of *Carex* and several other plants. It was earlier described under the name *Ciboria armeriae* by Von Höhnel (Frag. Myk. 22, Mitt. No. 1122, p. 43. 1918). This fungus is clearly not a *Sclerotinia*. It is without doubt a species of *Rutstroemia*.

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LITERATURE CITED

References cited in the text but not in the following list will be found in the synonymy of the species referred to.

Bommer, E. & **M. Rousseau.** *P. curreiana* Tul. *In* Florule mycologique des Environs de Bruxelles. Mem. Soc. Roy. Bot. Belg. **23:** 133. 1884.

Boudier, E. Icones Mycologicae **1–4.** 1905–1910.

Drayton, F. L. The sexual mechanism of Sclerotinia gladioli. Mycologia **26:** 48–72. 1934.

Ferdinandsen, C. & O. Winge. Studier over en hidtil upaaagtet, almindelig dansk Baegersvamp, Sclerotinia scirpicola Rehm. Biol. Arbejder Tilegnede, Eug. Warming den 3. November 1911: 281–298. 1911.

————. Über Myrioconium Scirpi Syd. Ann. Myc. **11:** 21–24. 1913.

Fries, E. *Peziza ciborioides. In* Observationes Mycologicae **2:** 307. 1824.

Groh, Herbert. A new host for Claviceps. Mycologia **3:** 37–38. 1911.

Höhnel, F. von, Über Epidocium affine Desmazières. Mitt. Bot. Inst. u. Tech. Hochsch. Wien **3:** 50–51. 1926a.

————. Über Placosphaeria Junci Bubák. Mitt. Bot. Inst. u. Tech. Hochsch. Wien **3:** 49–50. 1926b.

Lambotte, E. *Scler[otinia] curreiana* Tul. *In* Fl. Myc. Belg. Suppl. 1, p. (303). 1887.

Larsen, P. 324 *S. Vahliana* Rostrup, Grönl. Svampe 1891, p. 607. *In* Fungi of Iceland. *In* Rosenvinge & Warming, The Botany of Iceland 2^3: 504. 1932.

Lind, J. *Sclerotinia Curreyana* (Berk.) Karsten. *In* Danish Fungi as represented in the Herbarium of E. Rostrup, p. 108–109. 1913.

Massee, G. *Sclerotinia Curreyana. In* British Fungus-Flora **4:** 282–283. 1895.

Persoon, C. H. *(Peziza) Friesii. In* Mycologia Europaea **1:** 277. 1822.

Rostrup, E. *Sclerotinia Vahliana* Rostr. *In* Islands Svampe. Bot. Tidskr. $\mathbf{25}^3$: 315. 1903.

————. Fungi collected by H. G. Simmons on the 2nd Norwegian Polar Expedition, 1898–1902. *In* Rept. Second Norwegian Arctic Exped. in the "Fram" 1898, **9:** 5. 1906.

Saccardo, P. *Sclerotium nigricans* (Tul.) Sacc. *In* Syll. Fung. **14:** 1153. 1899.

————. *Sclerotinia Curreyana* (Berk.) Karst. *In* Syll. Fung. **8:** 198–199. 1889.

Tulasne, L. R. & C. Tulasne. Selecta Fungorum Carpologia **1:** 103–105. 1861; **3:** 203, pl. 22. 1865. (Transl. by W. B. Grove **1:** 106–108. 1931; **3:** 202, pl. 22. 1931).

Velenovsky, J. Monographia Discomycetum Bohemiae **1:** 1–436; **2:** *pl. 1–31.* 1934.

Whetzel, H. H. North American species of Sclerotinia II. Two species on Carex, S. duriaeana (Tul.) Rehm, and S. longisclerotialis n. sp. Mycologia **21:** 5–32. 1929.

————. The spermodochidium, an unusual type of spermatial fruit-body in the Ascomycetes. Mycologia **35:** 335–338. 1943.

————. Saccardo's confusion of the spermatial stage of S. duriaeana and S. curreyana with the sphacelia stage of Claviceps nigricans. Mycologia **36:** 426–428. 1944.

Whetzel, H. H. & W. G. Solheim. Sclerotinia caricis-ampullaceae, a remarkable subarctic species. Mycologia **35:** 385–398. 1943.